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A Floral and Faunal Inventory of the Réserve Naturelle Intégrale d'Andohahela, Madagascar: With Reference to Elevational Variation

Steven M. Goodman, Editor

June 30, 1999

Publication 1503

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A series of errors were introduced into this publication associated with corrections made on the page proofs that were not properly taken over at various production stages.

- p. viii, line 4—read “Réserve” as “Réserve”
- p. 47, column 2, line 19—read “Biologic” as “Biologie”
- p. 60, under relative density, plot 4—read “*Polysacias*” as “*Polyscias*”
- p. 67, under Florsitic Parameters, line 11—read “*aprevali*” as “*aprevalii*”
- p. 73, line 13—the value of “1.40” should be under column for plot 3, 1150 m
- p. 73, line 14—read “13.36” as “13.65”
- p. 74, line 19—read “*Polyathia*” as “*Polyalthia*”
- p. 74, lines 30—39—read “*Polycias*” as “*Polyscias*”
- p. 74, line 49—read “*Rhodocolea*” as “*Rhodocolea*”
- p. 75, line 72—the value “15.54” should be in bold print
- p. 76, lines 120—121—read “*Albizia*” as “*Albizia*”
- p. 76, line 163—read “*trichophebia*” as “*trichophlebia*”
- p. 78, lines 241—242—read “*Sizygium*” as “*Syzygium*”
- p. 78, line 293—read “*Schysmatoclada*” as “*Schismatoclada*”
- p. 79, line 309—the value “17.85” should be in bold print
- p. 84, lines 2—3 of table—read “*Chrysophyllum boivinianum*” as “*Chrysophyllum boivinianum*”
- p. 84, line 20—read “*Albizzia*” as “*Albizia*”
- p. 84, line 34—read “*Caesaria*” as “*Casearia*”
- p. 84, line 37—read “*Sizygium*” as “*Syzygium*”
- p. 85, line 11 from bottom—read “*Strebulus*” as “*Streblus*”
- p. 86, line 6 of table—read “*trichophebia*” as “*trichophlebia*”
- p. 87, line 4 of table—read “*Zanthoxylum*” as “*Zanthoxylum*”
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- p. 87, line 21 from bottom of table—read “*pervillena*” as “*pervilleana*”
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- p. 98, column 2, under Sample Sites, line 10—read “*Potamya*” as “*Potamyia*”
- p. 210, column 1, line 9—read “RS d’Anjanaharibe-Sud, or” as “RS d’Anjanaharibe-Sud.”
- p. 246, caption to Table 14—read “for five reserves” as “for four reserves”
- p. 248, Goodman and Rakotoarisoa reference—read “2—4” as “3—4”

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**A Floral and Faunal Inventory
of the Réserve Naturelle Intégrale
d'Andohahela, Madagascar**



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NEW SERIES, NO. 94

A Floral and Faunal Inventory of the Réserve Naturelle Intégrale d'Andohahela, Madagascar: With Reference to Elevational Variation

Steven M. Goodman, Editor

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Preface

This volume contains the results of a faunal and floral inventory conducted in extreme southeastern Madagascar in the Réserve Naturelle Intégrale (RNI) d'Andohahela between 3 October and 15 December 1995. This project was the third of five intensive multidisciplinary surveys, completed to date, conducted along elevational transects of mountainous regions on Madagascar. These surveys were coordinated by the World Wide Fund for Nature (WWF), Madagascar, and this volume is the third published in this series in *Fieldiana: Zoology*. The other two include the inventory of RNI d'Andringitra conducted in 1993 (*Fieldiana: Zoology*, n.s. 85) and that of the Réserve Spéciale (RS) d'Anjanaharibe-Sud in 1994 (*Fieldiana: Zoology*, n.s. 90). The results of subsequent altitudinal surveys are currently in preparation and include the RS de Marojejy in 1996 and the RS d'Ivohibe in 1997.

We are indebted to WWF staff in both Antananarivo and Tolagnaro for their help in organizing this mission, in particular Lalaniaina Andriamanarivo, Mark Fenn, Roland Laha, Olivier Langrand, Sheila O'Connor, Mamy Ravokatra, Tiana Razafimahatratra, and Malalarisoa Razafimpahanana. The assistance and cooperation of inhabitants of the villages of Enosiary and Eminiminy were extremely important for the success of the mission. It is with great pleasure that we acknowledge the work of M. Ledada Rachel Razafindravao, the *chef de cuisine*, who kept us well-fed under rather difficult conditions. Jean-Aimé Rakotoarisoa kind-

ly examined and dated pottery remains found within the reserve. We are also grateful to the Direction des Eaux et Forêts and the Association Nationale pour la Gestion des Aires Protégées, especially Célestine Ravaoarimomanga and Miodona Harisoa Faramalala, for permits to work in the reserve.

This volume has benefited greatly from the critical commentaries offered by numerous reviewers who evaluated the chapters presented herein. Those reviewers who did not waive anonymity are mentioned in the acknowledgments of each chapter. John Weinstein, Field Museum of Natural History, helped greatly in preparing the photographs. We continue to be indebted to William Burger, Scientific Editor of *Fieldiana*, and Marjorie Pannell, Managing Editor of the Field Museum Press, for accepting the arduous task of producing these volumes. Their organizational and editorial skills have graced these monographs. The 1995 biological inventory of the RNI d'Andohahela was made possible by a grant from USAID to WWF as part of an integrated conservation and development project aiming to protect the Andohahela region. Publication of this volume was significantly aided by generous grants from USAID and The Schlinger Foundation.

Steven M. Goodman
April 1998
Antananarivo

Note added in proofs: Over the past few months the status of several Malagasy reserves has changed, based on national decrees. We were unable to modify the text of this volume to reflect these changes. The Réserves Naturelle Intégrale d'Andohahela, de Marojejy, and d'Andringitra are now the Parcs National d'Andohahela, de Marojejy, and d'Andringitra, respectively.—S.M.G., 21 December 1998.

Chapter 1

Description of the Réserve Naturelle Intégrale d'Andohahela, Madagascar, and the 1995 Biological Inventory of the Reserve

Steven M. Goodman¹

Madagascar is well known for a remarkable variety of habitats, from lush rain forests to subdesert spiny bush forest. The Réserve Naturelle Intégrale (RNI) d'Andohahela is located in extreme southeastern Madagascar, in a zone of dramatic ecotones between the humid eastern and the dry southern portions of the island. Much of this habitat diversity is represented in the RNI d'Andohahela, largely as a result of the effect of the Anosyenne Mountains, which act as a rain barrier (Battistini, 1964; Goodman et al., 1997). The abrupt shift in habitats is due to this north-south-aligned mountain chain. The eastern slopes of these ancient mountains are a relatively short distance from the Indian Ocean coast, with their summital zone and higher ridges blocking the movement of rain-bearing clouds coming in from the east (Paulian et al., 1973). The biological communities occurring on either side of this divide have little in common with one another, and these differences are discussed in this volume.

The reserve, comprising 76,020 ha, is divided into three noncontiguous parcels (Nicoll & Langrand, 1989; Fig. 1-1): parcel 1 (humid forests on the eastern flank of the Anosyenne Mountains), between 46°37'–46°52'E and 24°30'–24°52'S—63,100 ha; parcel 2 (dry spiny forest and some degraded gallery forest along river margins to the west of the Anosyenne Mountains), between 46°33'–46°38'E and 24°48'–24°58'S—12,420 ha; and parcel 3 (transitional humid and dry forest located just to the west of the Anosyenne Mountains), between 46°37'–46°39'E and 24°59'–25°02'S—500 ha. The initial 30,000 ha of the re-

serve was established in 1939 after the botanical explorations of H. Humbert (1935, 1941). In 1966 an additional portion of the regional forest was placed within this protected area (Nicoll & Langrand, 1989).

The abrupt ecotone between wet and dry across this zone gives rise to an extraordinary level of species turnover in the biotic communities over the distance of a few kilometers. To emphasize this dramatic effect, I excerpt entries made in my field notebook during a December 1992 hike with Mark Pidgeon and Sheila O'Connor in parcel 1 of the reserve between Eminiminy and Mahamavo along the Isedro Trail:

In the early afternoon after climbing over the Col d'Ambatomanaha along the Isedro Trail we came to the final ridge before the descent down the western slopes of the Anosyenne Mountains . . . The ridge, the western limit of parcel 1, forms the ecotone between humid and dry forest of the reserve. Here we were surrounded by large trees and terrestrial leeches [characteristic of humid forests below 1200 m]. Just below we could see to the west a dramatic shift in vegetation. Large baobabs were within a kilometer or so of us and with binoculars the characteristic cactus-like *Didiereaceae* of the spiny bush forest could be seen in the not so far distance. The calls of humid forest birds were all around us, while those characteristic of spiny bush could be heard just below. The shift is so abrupt that it seemed possible to stand in the humid forest and throw a rock into the spiny bush.

Another interesting aspect of the region is that although all of the RNI d'Andohahela falls south of the Tropic of Capricorn, parcel 1 of the reserve retains characteristic aspects of a tropical humid or rain forest flora in both structure and species composition. This parcel is one of the southernmost "tropical" forests in the Old World.

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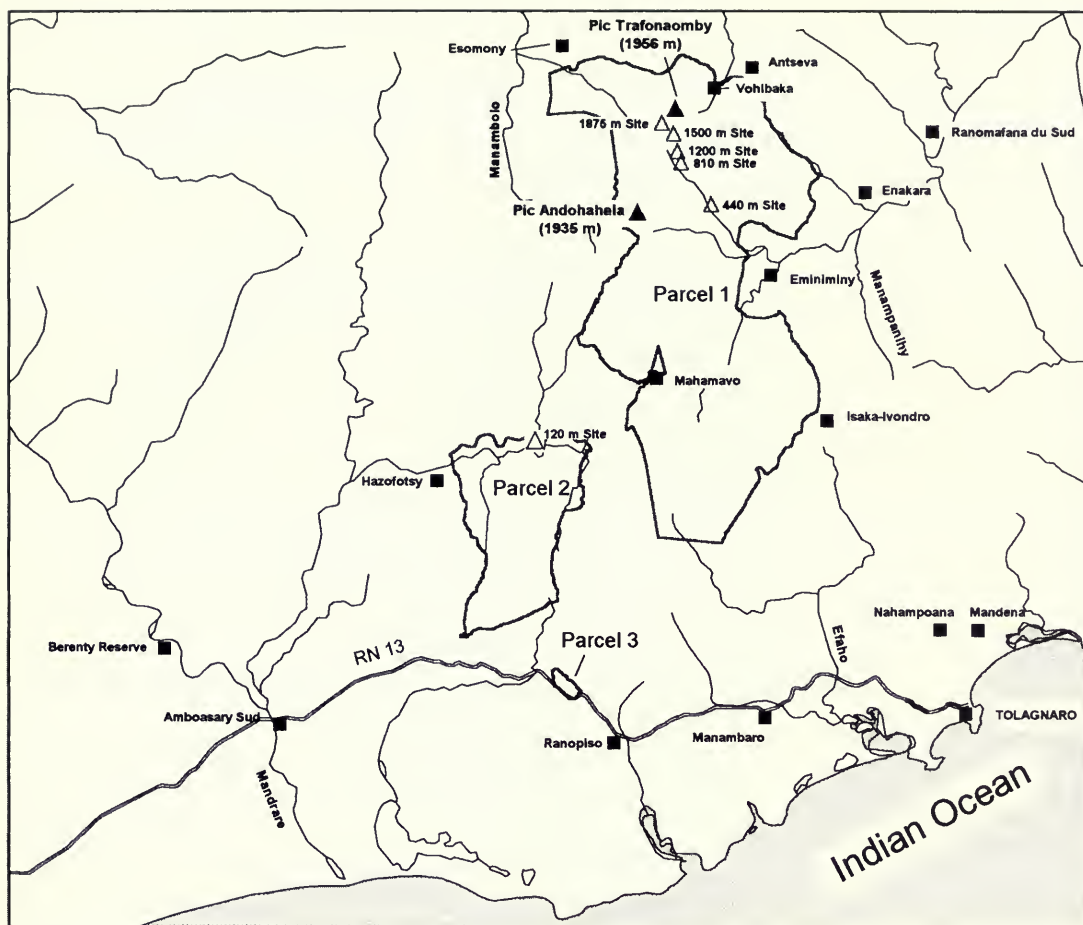


FIG. 1-1. Map of extreme southeastern Madagascar showing the position of the three parcels of the RN1 d'Andohahela and the positions of our transect sites during the 1995 inventory of the reserve. The map was designed by the GIS Unit, WWF, Madagascar.

A group of field scientists from seven different countries, representing numerous fields of interest in the fields of botany and zoology, studied the biota of the reserve between 19 October and 15 December 1995. Five camps were placed in parcel 1 at different elevational zones (440, 810, 1200, 1500, and 1875 m) along the humid eastern flank

and summital zone of the Anosyenne Mountains. One site in the gallery and spiny forest of parcel 2 (at 120 m) was also studied. Each site was occupied for a minimum of 8 days. The results presented in this volume are largely confined to parcels 1 and 2. All of the groups studied and collected during this mission are reported on herein;

the single exception is the report for the terrestrial snails. Many of the mission members and virtually all of the field methods were identical to those on similar transects conducted in the RNI d'Andringitra (Goodman, 1996), the Réserve Spéciale (RS) d'Anjanaharibe-Sud (Goodman, 1998), the RNI de Marojejy in 1996 (Goodman, in prep.), and the RS d'Ivohibe and the corridor linking that reserve to the RNI d'Andringitra in 1997 (Goodman, in prep.). We are currently organizing a mission to the RS de Manongarivo for the upcoming 1998 field season.

In this chapter details are presented on the 1995 expedition to the RNI d'Andohahela, along with some data on the climate, geology, and scientific exploration of the area. For more information on the RNI d'Andohahela readers are referred to O'Connor et al. (1985), Nicoll and Langrand (1989), and Goodman et al. (1997).

Abbreviations Used in the Text

ANGAP	Association Nationale pour la Gestion des Aires Protégées, Antananarivo
BM(NH)	The Natural History Museum, London (formerly British Museum [Natural History])
CNRE	Centre National de Recherche sur l'Environnement, Antananarivo
CNRS	Centre National de la Recherche Scientifique, Antananarivo
dbh	diameter at breast height
DEF	Direction des Eaux et Forêts
FAC	Fonds d'Aide et de Coopération
FMNH	Field Museum of Natural History, Chicago
FTM	Foiben-Taosarintanin'i Madagasikara, Antananarivo (Institut National de Géodésie et Cartographie)
LRSAE	Laboratoire de Recherche sur les Systèmes Aquatiques et leur Environnement, Antananarivo
MBG	Missouri Botanical Garden, St. Louis
MNHN	Muséum National d'Histoire Naturelle, Paris
MRAD	Ministère de la Recherche Appliquée au Développement, Antananarivo
ORSTOM	Institut Français de Recherche pour le Développement en Coopération (formerly Office de la Recherche Scientifique et Technique Outre-Mer)

PBZT	Parc Botanique et Zoologique de Tsimbazaza, Antananarivo
PN	Parc National
RB	Réserve de Biosphère
RCP	La Recherche Coopérative sur Programme No. 225, under the Centre National de la Recherche Scientifique
RNI	Réserve Naturelle Intégrale
RS	Réserve Spéciale
UMMZ	University of Michigan Museum of Zoology, Ann Arbor
USNM	National Museum of Natural History, Washington, D.C. (formerly United States National Museum)
WWF	World Wide Fund for Nature

Transect Sites

During our 1995 inventory of the reserve, coordinates for each transect site were determined with the use of a geographical positioning system, and the names for various localities were taken from maps (Institut Géographique National, 1961a,b; FTM, 1979, 1990) and discussions with local people. A gazetteer of the localities mentioned in the text is presented at the end of this volume (page 285). The first four transect zones in parcel 1 of the reserve ranged generally ± 75 m in elevation relative to and centered around our first four camps. Due to problems associated with access to water and the lack of a relatively flat zone in which to install a large number of people, our fifth camp was not the center of the transect but established north of Pic Trafonaomby, at about 1700 m. The fifth and final transect site in parcel 1 was at 1875 m ± 75 m. In parcel 2 there was little topographic variation.

Elevations were determined with the use of altimeters. The positions of each camp during the survey are indicated in Figure 1-1.

Parcel 1

- 440 m (camp 1) 19–28 October 1995—Madagascar: Province de Toliara, Réserve Naturelle Intégrale d'Andohahela, 8 km NW of Eminiminy, 46°45.9'E, 24°37.6'S
- 810 m (camp 2) 28 October–7 November 1995—Madagascar: Province de Toliara, Réserve Naturelle Intégrale d'Andohahela, 12.5 km NW of Eminiminy, 46°44.3'E, 24°35.6'S

1200 m (camp 3) 7–17 November 1995—Madagascar: Province de Toliara, Réserve Naturelle Intégrale d'Andohahela, 13.5 km NW of Eminiminy, 46°44.1'E, 24°35.0'S.

1500 m (camp 4) 17–27 November 1995—Madagascar: Province de Toliara, Réserve Naturelle Intégrale d'Andohahela, 15.0 km NW of Eminiminy, 46°43.9'E, 24°34.2'S.

1875 m (camp 5) 27 November–5 December 1995—Madagascar: Province de Toliara, Réserve Naturelle Intégrale d'Andohahela, 20.0 km SE of Andranondambo, 46°43.3'E, 24°33.7'S.

Parcel 2

120 m (camp 6) 7–15 December 1995—Madagascar: Province de Toliara, Réserve Naturelle Intégrale d'Andohahela, 7.5 km ENE of Hazofotsy, 46°36.6'E, 24°49.0'S.

Itinerary of the 1995 Expedition

Before our inventory of parcel 1 of the RNI d'Andohahela, two trails existed that traversed the northern portion of this forest. The Enakara–Antseva Trail formed, in part, the northern boundary of the parcel and cut across the Marosohy Forest; the Eminiminy–Mahamavo Trail (also known as the Isedro Trail) passed via the Col d'Ambatamaniha. Neither of these paths approached the summital zone of the Anosyenne Mountains, however, and it was decided that a new trail needed to be created that linked the lowest-lying areas of the parcel with the summit of Pic Trafonaomby (1956 m).

Over the course of numerous trips to the region between May and September 1995, P. J. Rakotomalaza and N. Messmer conducted extensive reconnaissance trips in collaboration with local villagers, and they were able to establish a trail system that ran from the west of Eminiminy at about 300 m, entered the forest slightly below 400 m, and continued in a northwesterly direction up to about 1500 m. Four camps were set up along this trail at 440, 810, 1200, and 1500 m. The means to reach the summital zone was established from the 1500 m camp. Our fifth transect was at 1875 m, just below Pic Trafonaomby. The fifth camp was northwest of the peak, in a relatively flat area

with running water, and about 2–2.5 km from the fifth transect zone.

During the field mission (19 October–15 December 1995), members of the scientific group included F. Andriatsiferana (botany), J.-M. Elouard (aquatic insects at the 440 and 810 m sites only), A. Feistner (lemurs), S. M. Goodman (small mammals, birds, and bats), A. F. A. Hawkins (birds), N. Helme (botany), R. Laha (botany and logistics), N. Messmer (botany), J. M. Rakotoarison (terrestrial snails in parcel 1 only), P. J. Rakotomalaza (botany), F. Rakotondrainibe (ferns), J.-B. Ramanamanjato (reptiles and amphibians), B. Randriamampionona (ferns), A. Raselimanana (reptiles and amphibians), M. Ravokatra (birds), M. Pidgeon (small mammals and carnivores), and J. Schmid (lemurs). Including scientific staff, assistants, and visitors, the number of people inhabiting various camps reached a maximum of 24. Numerous other scientists participated in the determination of specimens and analysis of data obtained during the 1995 field survey. In addition, based on an earlier field trip to another area of parcel 1, a chapter by B. L. Fisher on the ants of RNI d'Andohahela is included in this volume. The names and addresses of all field and laboratory researchers involved in this project are given at the end of this chapter (Appendix 1-1).

Logistics and Trail Systems

Parcel 1 of the RNI d'Andohahela is not accessible by motor vehicle. An old road that terminated at Eminiminy has not been passable for several decades. Access to the eastern edge of the parcel was by a foot trail that began just slightly north of Isaka-Ivondro on the road linking the Tolagnaro area to Manantenina via Ranomafana du Sud. This trail, known as the Tananana Trail, starts at 85 m, climbs up to the Col de Tananana (approximately 750 m), then drops into the Manampanihy River Valley and to the villages of Eminiminy and Enosiary at about 300 m. These two villages were used as bases for the transfer of food reserves, supplies, and specimens during our mission, and the majority of porters employed during the displacements between camps (up to 40 individuals) were from these two villages.

Food and research supplies were divided by camp (transect zone), packed in rice sacks, and stored in the WWF office in Tolagnaro. Two days before each scheduled camp shift, a WWF em-

ployee in Tolagnaro purchased fresh food in the local market and transported these goods and the stored supplies for the next camp by car to Isakalivondro. From there porters were engaged to carry the material to Enosiary (via the Tananana Trail), a 5-hour trip. The following morning porters from Enosiary and Eminiminy carried the supplies to the site we were preparing to leave. There the baggage was rearranged, and the research group with porters climbed to the next site. After the second camp the distances were too long for the Enosiary/Eminiminy porters to make the round-trip over the course of 1 day, and makeshift camps had to be installed along the trail with cooking pots and food to accommodate the porters for the night. Between Eminiminy and our last camp near Pic Trafonaomby, the round-trip for the porters took 3 or 4 days.

As mentioned earlier, in order for the research group to have access to the summital zone of parcel 1 of the RNI d'Andohahela it was necessary to open and establish a new trail system. A pre-existing trail that entered a short distance into the forest was used to access the reserve to the east of Eminiminy. The site of our first camp at 440 m was along the Andranohela River in an area of forest that showed ancient signs of human disturbance, including old tombs and certain aspects of the flora that indicated old secondary growth. This area of the reserve is occasionally visited by villagers to exploit various forest products, such as medicinal plants and honey, as well as for hunting. Above our first camp the preexisting trail ended; here P. J. Rakotomalaza and N. Messmer began their efforts to establish a new trail system toward Pic Trafonaomby.

The trail linking camp 1 (440 m) to camp 2 (810 m) passed along a series of undulating hills that climbed slowly in altitude. The trail crossed numerous small streams, some perennial and others seasonal, and areas with large granitic boulders. The camp was located along a tributary of the Andranohela River in a relatively deep valley surrounded by intact forest. Although we were initially under the impression that this forest was undisturbed, pottery dating from the 15th or 16th century was found at the site (Goodman & Rakotoarisoa, in press). Furthermore, there is a rich modern oral history associated with human occupation of the area (Charles, 1985; Razanabahiny, 1995; Rakotoarisoa, 1998) that probably dates from the same period as the pottery. Thus, although no modern trails exist in this area of the forest, it was formerly frequented by humans.

Our third camp, at 1200 m, was on a ridge above the Andranohela River in a zone with relatively steep slopes. Here there was a marked change in topography from the relatively flat valley basins associated with the lowlands, particularly at camp 1, to the generally sharp topography and often narrow ridges leading up to the summital region of the Anosyenne Mountains. From just above camp 2 to near Pic Trafonaomby, no sign of recent or past human occupancy or utilization of the forest was found.

Access to the fourth camp, at 1500 m, was via a narrow ridge that climbed abruptly above the 1200 m camp. The 1500 m site was in a sort of hanging valley or steppe below the steep slopes leading to the summital zone. Sufficient flat ground and running water were found in this valley to establish our camp. Numerous small rivers drained the basin, coalesced, and then dropped off the valley in a series of waterfalls that formed the headwaters of the Andranohela River.

Pic Trafonaomby (1956 m) is a small dome that rises from a narrow and gently sloping plateau at about 1875 m, and the fifth transect was centered on this plateau. Because of lack of running water in this immediate area, it was necessary to establish our camp associated with the 1875 m transect in an area to the north, about 2–2.5 km from the study zone. The campsite was in an isolated forest fragment with a small running stream, and just above a marsh known locally as Ankebotsy.

The limit of the continuous forest that we had entered weeks earlier above the village of Enosiary was found to the north of the plateau below Pic Trafonaomby. This disturbed region, although still within parcel 1, had been opened up for cattle pasture and is regularly burned to provide new forage. The lower slopes to the north and west, outside of the reserve, are largely anthropogenic grasslands with a few remnant islands of forest. Herders with their animals from the high mountain villages, such as Vohibaka and Antseva, and those on the lower slopes to the west, such as Esomony, regularly pass through this zone. Days before our arrival at the site around the 1875 m transect, a fire had been set that entered into the forest and seriously damaged the understory of an area approximately 3–4 ha in size.

After discussion with local cattle herders that frequented Ankebotsy, it became clear that it was possible to exit parcel 1 via the western slopes of the Anosyenne Mountains. This route takes approximately 5 hours to walk and leads to Esomony, where we were met by vehicles. After 7

TABLE 1-1. Summary of minimum and maximum temperatures and precipitation during 1995 expedition to RNI d'Andohahela.

Periods of measurement within each transect	Temperature (°C)*		Rainfall (mm)†
	Minimum	Maximum	
Parcel 1			
440 m 19–28 Oct.	7, 16.5–20.0, 17.0 ± 1.22	7, 26.0–28.5, 27.9 ± 0.87	3, 0.2–27.5, 12.5 ± 11.29
810 m 28 Oct.–7 Nov.	9, 11.0–14.0, 12.0 ± 1.05	9, 15.5–29.0, 23.6 ± 4.89	5, 0.1–4.0, 1.5 ± 1.33
1200 m 7–17 Nov.	10, 11.5–16.5, 14.4 ± 1.53	9, 21.5–26.5, 24.6 ± 1.78	1, 0.7
1500 m 17–27 Nov.	10, 9.0–15.5, 13.2 ± 1.64	9, 16.0–21.5, 18.0 ± 2.29	8, 0.5–11.0, 5.9 ± 6.00
1875 m‡ 27 Nov–5 Dec.	7, 6.0–12.0, 9.1 ± 2.03	6, 11.0–25.5, 18.8 ± 5.50	6, 0.5–17.5, 5.0 ± 6.0
Parcel 2			
120 m 7–15 Dec.	8, 14.0–22.0, 18.4 ± 2.38	7, 28.0–37.5, 33.8 ± 2.75	2, 0.5–1.0

* Data are presented as number of records, range, mean, and SD.

† Data are presented as number of days with rain, range, mean, and SD.

‡ Weather station installed within transect zone rather than near camp.

weeks of intensive fieldwork, the Esomony option, rather than the 3-day walk back to where we had entered parcel 1, was ideal. Two days before our final displacement from parcel 1, a member of our group descended to Esomony to organize the porters.

The final site visited was in parcel 2 of the reserve in an area of spiny bush forest to the east-northeast of Hazofotsy. The camp, just a few tens of meters outside the northern limit of parcel 2, was accessible by vehicle and was along a tributary of the Mananara River. The forest, most of which was in the reserve, had an extensive trail system.

Meteorology

The principal factor giving rise to the remarkable habitat variation of the RNI d'Andohahela is the dramatic difference in annual precipitation between the eastern and western sides of the Anosyenne Mountains (Ratsivalaka-Randriamanga, 1985, 1987). The moisture-laden weather systems that move into the region from the east to the west are trapped by the windward side of the Anosyenne Mountains (Paulian et al., 1973). The leeward side receives considerably less precipitation. "Over the distance of some sixty kilometres as

the crow flies, there is a transition from mean rainfalls of less than 600 mm to amounts in excess of 1500 mm" (Donque, 1972, p. 136). This shift in rainfall is much more abrupt than Donque described, but owing to a lack of meteorological stations in transition areas, it is impossible to be more precise (Paulian et al., 1973; Donque, 1975; Goodman et al., 1997). Mean annual temperatures are distinctly higher to the west of the Anosyenne Mountains than to the east. More details are presented on the regional climate by Paulian et al. (1973).

Along the eastern slopes of the Anosyenne Mountains, covering an elevational range from near sea level to over 1900 m, there is considerable variation in both rainfall and temperature. Weather stations do not exist along this gradient. Data collected on the minimum and maximum daily temperatures (°C) and daily precipitation during the 1995 expedition to the RNI d'Andohahela can be used to partially examine variation along the eastern slope of this range (Table 1-1).

As expected, shifts in daily minimum and maximum temperatures showed elevational differences, with the warmest temperatures being in the lower-lying areas and the coldest temperatures toward the summital zone. Temperatures at the 1200 m site, however, were on average warmer than those at the 810 m site. Whether this difference

is a question of chance related to passing weather systems during our stay in each zone or is an orographic effect is unknown. We had more rainy days at the upper two camps; it rained for 8 of 10 days at 1500 m and 6 of 7 days at 1875 m. This portion of the mountain was often shrouded in clouds and mist for a good portion of the day. We strongly suspect that this pattern was not a temporal shift related to seasonal changes as we moved up the slopes over the course of the inventory, but rather associated with air circulation over the Anosyenne Mountains (Humbert, 1935).

The weather in parcel 2 at the 120 m site was generally clear and warm (Table 1-1). Little rain fell during our 9-day stay at the site. The major exception was a very heavy rain that occurred moments after we arrived at the site. This downpour occurred before the rain gauge had been installed, but an estimated 20–30 mm of rain fell over the course of 40 minutes.

Geology

Parcel 1 of the RNI d'Andohahela is dominated by the Anosyenne Mountains. This mountain chain runs, at its southern limit, from just west of Ranopiso north to the Isandra Valley at the base of the Midongy-Sud Massif (Battistini, 1964; Paulian et al., 1973). The range is formed from Precambrian gneiss and granitic rocks, and their deposited alluvium is lateritic or ferrallitic soils (Bourgeat, 1972). The eastern slopes form the drainage for the Efaho and Manampanihy rivers and the western slopes for the Mananara and Mandrare rivers.

To the west of the Anosyenne Mountains, including parcel 2 of the RNI d'Andohahela, is a large basin with little relief and largely xerophilous vegetation. Soils shift abruptly from the lateritics of the mountains to siliceous sands. The region is geologically complex, with the juxtaposition and infolding of numerous formations (Noizet, 1953). For more detailed information on the geology of the region see Battistini (1964), Besairie (1970), Brenon (1972), Paulian et al., (1973), and Goodman et al. (1997).

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- Goodman, S. M., Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, Illinois 60605-2496, U.S.A., and World Wide Fund for Nature, Aires Protégées, B.P. 738, Antananarivo (101), Madagascar.
- Hawkins, A. F. A., B.P. 8511, Antananarivo (101), Madagascar.
- Helme, N. A., 189 Main Road, Kalk Bay, 7975, South Africa.
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- Nussbaum, R. A., Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48109-1079, U.S.A.
- O'Connor, B. M., Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48109-1079, U.S.A.
- Oliarinony, R., Laboratoire de Recherche sur les Systèmes Aquatiques et leur Environnement (LRSAE), ORSTOM, B.P. 434, Antananarivo, Madagascar.
- Messmer, N., Conservatoire et Jardin Botaniques de la Ville de Genève, Case Postale 60, CH-1292 Chambésy/Genève, Switzerland.
- Pidgeon, M., World Wide Fund for Nature, B.P. 738, Antananarivo (101), Madagascar. *Current address*: Route de St. Cergue, 1270 Trélex, Switzerland.
- Pilaka, T., Laboratoire de Recherche sur les Systèmes Aquatiques et leur Environnement

- (LRSAE), ORSTOM, B.P. 434, Antananarivo (101), Madagascar.
- Rakotoarison, J. M., Institute for the Conservation of Tropical Environments, B.P. 3715, Antananarivo (101), Madagascar.
- Rakotomalaza, P. J., Missouri Botanical Garden, B.P. 3391, Antananarivo (101), Madagascar.
- Rakotondrainibe, F., Ecole Pratique des Hautes Etudes, 16, rue de Buffon, 75005 Paris, France.
- Ramanamanjato, J.-B., Département de Biologie Animale, Université d'Antananarivo, B.P. 906, Antananarivo (101), Madagascar.
- Randriamampionina, B., World Wide Fund for Nature, B.P. 42, Tolagnaro (614), Madagascar.
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- Current address:* World Wide Fund for Nature, B.P. 738, Antananarivo (101), Madagascar.
- Ravokatra, M., World Wide Fund for Nature, B.P. 738, Antananarivo (101), Madagascar.
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- Sartori, M., Musée Cantonal de Zoologie, CP 448, CH-1000, Lausanne 17, Switzerland.
- Schmid, J., Deutsches Primatenzentrum, Kellnerweg 4, Göttingen 37077, Germany, and Abteilung für Verhaltenphysiologie, Beim Kupferhammer 8, 72070 Tübingen, Germany.

Chapter 2

An Overview of the Botanical Communities of the Réserve Naturelle Intégrale d'Andohahela, Madagascar

Nick A. Helme¹ and Pierre Jules Rakotomalaza²

Abstract

An outline of the botanical communities of the Réserve Naturelle Intégrale d'Andohahela is presented. The study area was centered on an elevational transect between 440 and 1950 m along the eastern slopes of parcel 1 of the reserve, and also within a limited area of the spiny bush forest of parcel 2 at 120 m. A shift in species composition of pteridophytes and, somewhat less pronouncedly, in angiosperms occurred between the first (420 m) and second (810 m) transect zones, apparently reflecting a shift from humid lowland to mid-altitude forest, but a true mid-elevation montane community was not present below 1000 m. Monocarpic Acanthaceae and bamboo tended to dominate the understory within the mid-altitude and montane zones (800–1800 m). The exposed ridges above 1200 m supported a distinct, small-leaved, sclerophyllous forest community characterized by low, gnarled trees that were covered in epiphytes. Large trees, up to 30 m tall, were recorded in the valleys at 1600 m, but they were significantly smaller above this elevation. The upper slopes (1800–2000 m) supported humid montane forest, with an abundance of both epiphytic and terrestrial mosses and ferns. Exposed rock was a feature of the highest elevations, where plant communities included *Philippia* scrubland and shallow-soil areas dominated by sedges and grasses. Parcel 2, which has low rainfall, had the typical spiny bush forest of the region. It was dominated by species of *Euphorbia* and *Didiereaceae*, with a dense, shrubby understory.

Résumé

Les communautés botaniques de la Réserve Naturelle Intégrale d'Andohahela sont présentées en grandes lignes dans ce chapitre. Le site d'étude est axé sur un transect altitudinal compris entre 440 et 1950 m d'altitude sur le versant oriental de la parcelle 1 de la réserve, ainsi que dans le fourré xérophile de la parcelle 2 de la réserve à 120 m d'altitude. Bien que peu marqué, un changement de la composition floristique, plus évident toutefois au niveau des ptéridophytes que des angiospermes, est observé entre le premier site d'étude (420 m) et le deuxième (810 m), reflétant le passage de la forêt dense humide de basse altitude vers la forêt de moyenne altitude. Une forêt de moyenne altitude typique n'est cependant pas observée en dessous de 1000 m d'altitude. Des espèces monocarpiques, des Acanthaceae et des bambous ont tendance à dominer le sous-bois des zones de moyennes altitudes et des forêts de montagnes (800–1800 m). Les crêtes exposées au-dessus de 1200 m incluent une forêt sclérophylle caractérisée par des arbres bas, tortueux, aux feuilles petites, et couverts d'épiphytes. En revanche, des arbres

¹ 189 Main Road, Kalk Bay, 7975, South Africa.

² Missouri Botanical Garden, B.P. 3391, Antananarivo (101), Madagascar.

atteignant presque 30 m de hauteur sont à nouveau observés dans les vallées à 1600 m. Au-dessus de cette altitude, la hauteur des arbres diminue significativement. Le versant entre 1800 et 2000 m est dominé par une forêt humide de montagne, riche en mousses et fougères épiphytes et terrestres. Les rochers exposés présentent des fourrés ericoïdes caractéristiques des plus hautes altitudes, et les zones à sol peu profond sont dominées par des Cyperaceae et des Poaceae. La parcelle 2 de la réserve quant à elle contient un fourré xérophile typique de cette région, dominé par des espèces d'*Euphorbia* et de Didiereaceae, et à sous-bois dense et arbustif.

Introduction

The earliest botanical exploration of the Andohahela Massif was carried out by Humbert (1935, 1941), who discovered some interesting species, mainly along the summital ridge. The results of his visits to the region formed the basis for establishing the Réserve Naturelle Intégrale (RNI) d'Andohahela. Various other botanists (Capuron, Cours Darne, and Saboureau) explored the lower western slopes of the massif but did not publish information regarding their botanical collections. No further studies were made in the forests of the eastern slope until the 1980s, when Missouri Botanical Garden (MBG) staff started a program in the area, concentrating on the lower slopes and adjoining ridges. Other than the initial exploration by Humbert, however, the mid-altitude and upper forests remained poorly known until the current expedition.

The RNI d'Andohahela is the most southerly example of Malagasy humid montane forest. The entire reserve, composed of three noncontiguous parcels, is south of the Tropic of Capricorn. Although the forests are thus not strictly tropical, they are of the same broad type as is found further north along the eastern escarpment of the island. Due to the topographic variation within parcel 1 (300–2000 m), three major phytogeographic domains (*sensu* Humbert, 1955) are represented: the Eastern Domain, or humid lowland forest (traditionally 0–800 m); the Central Domain, or mid-altitude humid forest (traditionally 800–2000 m); and the High Mountain Domain, or dwarf montane forest and heathland (usually above 1900 m). Du Puy and Moat (1996) slightly modified the classification of evergreen formations of eastern and central Madagascar, delimiting the zone of mid-altitude humid forest to 800–1800 m and referring to lower humid montane forest as that occurring from 1800 m to 2000 m. Their classification is not used in this chapter. A unique and important feature of the area is the phenomenal rainfall gradient from the upper slopes of parcel

1 (e.g., at the base of Pic Trafonaomby) toward the spiny forest in the west encompassing parcels 2 and 3. Over a horizontal distance of no more than 15 km, the average annual rainfall drops from an estimated 3,000 mm to 500 mm (Paulian et al., 1973), producing one of the most striking biotic gradients that can be seen anywhere in Madagascar (Goodman et al., 1997). Although none of our study sites were on these western slopes of parcel 1, most of which fall outside the boundaries of the reserve, it should be borne in mind that there are nevertheless some steep rainfall gradients within the relatively small area (63,000 ha) of parcel 1 of the RNI d'Andohahela. This summary focuses on the environmentally more homogeneous eastern slopes of parcel 1. It is by no means a definitive account of the entire reserve, owing to the presence of the abrupt habitat gradient on the leeward side of the mountain. Information is also provided on parcel 2, the dry, spiny forest portion of the reserve. For further details on the topography, climate, and geology of the reserve and information on study sites, see Chapter 1.

A further important feature of the eastern slopes of the RNI d'Andohahela is that the forests are still largely intact, providing a fine example of the unbroken transition from lowland to mid-elevation to eastern humid montane forest. Our lower two elevational sites, at 440 and 810 m, were located in areas that probably supported a small human population many centuries ago, while the upper three study sites were in apparently virgin forest. Although most of the forest at the lower sites was mature humid lowland forest, there were indications that certain areas had been disturbed several hundred years ago. In any case, the forest throughout the eastern slopes is essentially undisturbed today, with few preexisting trails, and there is no logging or subsistence agriculture (*tavy*) above about 300 m.

A detailed analysis of the structure, floristics, and phytogeography of the area, based largely on 1 ha plots, is presented in Chapter 4. This chapter

reviews the characteristic aspects of the vegetation and flora of the various elevational zones.

440 m

After leaving behind the last of the Enosiary rice paddies and open anthropogenic grasslands, at an altitude of about 300 m, we entered an area of disturbed forest, with numerous small lianas and traveler's palm (*Ravenala madagascariensis*). The forest at this low elevation appeared to be more deciduous than that growing slightly higher up the valley, in the vicinity of our study area, centered at 440 m. Various saxicolous plants such as *Kalanchoe* were seen growing on the enormous granite boulders that littered the valley. Our initial camp was located along the Andranohela River at an altitude of 440 m. The forest in the valley and along the lower slopes was structurally humid lowland forest, with a canopy of 15–20 m and a large component of buttressed, emergent species 25–30 m tall (Fig. 2-1). There was a high liana density, and although most were small, some enormous *Piper* lianas were recorded. Epiphytes were present, but by no means abundant; they included the bird's nest fern (*Asplenium nidus*), *Pothos scandens* (hemi-epiphytic Araceae), and various mosses that covered no more than 20% of the available surface area. Common emergents included *Dilobeia thouarsii*, *Chrysophyllum boivinianum*, *Sloanea rhodantha* var. *rhodantha* form *quadriloba*, and *Ocotea* spp. Canopy species included *Sorindeia madagascariensis*, *Ilex mitis*, *Syzygium* spp., *Oncostemum* spp., *Tambourissa* spp., *Diospyros* spp., *Polyscias* sp., *Dracaena reflexa*, *Dombeya* spp., *Treculia* sp., and various Rubiaceae. The understory was composed of numerous seedlings of the canopy species plus different *Tambourissa* spp., *Noronhia* sp., and various terrestrial ferns. There was a dense leaf litter in most areas. During our visit to this site, at the end of the dry season, the soil surface was dry, but some moisture occurred a few centimeters below the surface. Large palms were not particularly common or diverse, with only one *Ravenea* and two *Dypsis* spp. noted. Bamboo clumps were not an important feature of the forest at this elevation. *Dalbergia* spp. were uncommon, tending to have clumped distributions. Dominant families in the transect (trees with a dbh >10 cm) were Rubiaceae, Clusiaceae, Lauraceae, Elaeocarpaceae, and Myrsinaceae (Chapter 4, Table 4-5).

The rocky, fast-flowing clear water Andrano-

hela River supports a well-developed riparian forest at this elevation, with typical widespread riverine plants such as *Aphloia theiformis*, *Ficus* sp., *Antirrhoea* sp., *Weinmannia* spp., *Phyllanthus* spp., *Albizia* sp., *Micronychia* sp., and *Dombeya* spp. *Ravenala* was more common in light gaps along the river than in tall forest. The big black gneissic rocks along the river margins were worn smooth, but a number of grasses and small herbs, such as *Lobelia*, managed to find a foothold in sandy cracks. Below the waterline were large populations of the unusual subaquatic plant *Hydrostachys* sp., which flowers when the water level drops in the dry season. This genus of some 22 species is restricted to Africa and Madagascar, with most of the species being endemic to Madagascar. The riverine plant community is relatively constant at elevations below about 1000 m. Above this altitude genera such as *Ravenala* tended to drop out, being replaced by *Cyathea* in the narrower streambeds with their lower filtering light values.

810 m

The trail between 440 and 810 m was remarkable for its density of lianas. Numerous large granite boulders were present, and in certain areas away from the river the usually loamy soils became distinctly sandy, with a high content of large quartzitic crystals derived from the weathered granite. The trail crossed a number of small streams, the majority of them essentially seasonal, although two were perennial, with deep pools and large waterfalls plunging off the steep southeast-facing slopes. Our 810 m camp was situated at the confluence of a perennial tributary and the Andranohela River, and was surrounded on all sides by steep slopes clothed in dense, humid lowland forest (Fig. 2-2).

The flowering plant flora in the 810 m elevational zone was not dramatically different in structure or composition from that at 440 m. For pteridophytes this difference was much more notable. The fern community showed a distinct species turnover between the first (420 m) and second (810 m) transect zones (see Chapter 3) that apparently reflected a shift from humid lowland to mid-altitude forest. At 810 m in parcel 1 virtually all the emergent and large canopy trees had at least 20–50% epiphyte cover, with *Usnea* lichens, *Asplenium* ferns, and *Bulbophyllum* orchids dominating. The hemi-epiphytic *Pothos scandens*, so



FIG. 2-1. View of humid lowland forest at 440 m in parcel 1 of the RNI d'Andohahela. In this area the canopy height was generally 15–20 m, with emergent species reaching up to 25–30 m. There was a high liana density, and epiphytes were present but not abundant, covering less than 20% of the available surface area. The understory was composed of numerous seedlings of canopy species (*Sorindeia madagascariensis*, *Ilex mitis*, *Syzygium* spp., *Oncostemum*, *Tambourissa*, *Diospyros*, *Polyscias*, *Dracaena reflexa*, *Dombeya*, *Treculia*, and Rubiaceae), plus different *Tambourissa*, *Noronhia*, and terrestrial ferns. (Photograph by M. Pidgeon.)



FIG. 2-2. Tributary of the Andranohela River at about 820 m and just above our second camp in parcel 1 of the RNI d'Andohahela. The canopy height here was similar to that of the 440 m site, and emergent species consisted of *Sloanea rhodantha* var. *rhodantha* form *quadriloba*, a few scattered *Canarium obovatum*, *Dilobeia thouarsii*, *Ocotea*, Myrtaceae, and Moraceae. The majority of large trees had at least 20–50% epiphyte cover, and moss was common on vertical and horizontal branches. The understory was not dominated by a *Tambourissa* shrub as at 440 m, but by two species of Acanthaceae that reached 1.5 m in height. (Photograph by N. Helme.)

common at 440 m, had virtually disappeared. Moss was common on vertical and horizontal branches.

The canopy height at 810 m was similar to that at 440 m. Emergents averaged 20–30 m, while the main canopy was usually between 15 and 20 m. Emergents included the ubiquitous *Sloanea rhodantha* var. *rhodantha* form *quadriloba*, a few scattered *Canarium obovatum*, *Dilobeia thouarsii*, *Ocotea* spp., Myrtaceae spp., and Moraceae spp. The canopy was dominated by members of the Moraceae (*Trilepisium*, *Treculia*, *Streblus*), Myrtaceae (especially *Syzygium* spp.), and Monimiacae (*Tambourissa* spp.), and included other genera such as *Macaranga*, *Allophylus*, *Plagioscyphus*, *Filicium*, *Antidesma*, *Noronhia*, *Vepris*, *Polyscias*, *Oncostemum*, and various Clusiaceae.

The understory was dominated not by a *Tambourissa* shrub, as at 440 m, but by two species of Acanthaceae that reached 1.5 m in height. This domination by a monocarpic giant herb, which be-

came even more pronounced at higher elevations, is a feature of many paleotropical montane forest understories (Davis et al., 1994).

Bamboo (especially the lianescent *Nastus*) was fairly common and occasionally formed dense tangles, especially along light gap edges. There seemed to be fewer lianas than at 440 m. Various species of *Oncostemum* were common understory shrubs at elevations up to 1200 m, and their red berries were regularly seen being eaten by frugivorous birds such as *Philepitta castanea*. Large palms were rare at 810 m, although small understory species of *Dypsis* were common.

There was a high degree of heterogeneity in this zone, with remarkably different plant communities adjacent to each other, suggesting some strong environmental/edaphic gradients that were not immediately evident to us. Just north of our camp, for example, an area at the base of the ridge leading toward the 1200 m site was characterized by a more open understory with fewer liana tan-



FIG. 2-3. View of regenerating vegetation along natural landslide just above the Andranohela River at about 800 m in parcel 1 of the RNI d'Andohahela. The landslide probably occurred within the preceding 10–15 years, as judged by the size of the small trees, and it appeared to have been caused by water-saturated earth slumping down a relatively steep slope. The area is characterized by pioneer species such as the fern *Dicranopteris linearis*, the trees *Dombeya*, *Croton*, *Weinmannia*, and *Maesa*, and on drier, thinner soils by a species of *Philippia* and a tall *Helichrysum*. *Nastus* bamboos were common along the forest/landslide boundary. (Photograph by N. Helme.)

gles, species such as *Cyathea* (indicating moist, deep soils), patches of *Ivodea madagascariensis* (Rutaceae), and small *Dypsis* palms. The bamboo *Nastus* was common, its leaves often making up the bulk of the leaf litter. Large specimens of *Dalbergia* were more common than elsewhere (this also seemed to be their altitudinal limit), and they shared the canopy with *Dombeya*, *Grewia*, *Trilepisium*, *Macaranga*, *Brillantaisia madagascariensis*, *Filicium*, and *Allophylus*.

Another unusual habitat was formed by what was clearly regeneration on a landslide track (Fig. 2–3). Similar patches of vegetation could be seen throughout the study area, and although they were not abundant (perhaps one per 200 ha), they undoubtedly play an important role in the dynamics of the forest, providing regeneration opportunities for light gap species. One such area was visible along the river at 800 m, covering about 1.5 ha on a 50° slope. The landslide probably occurred relatively recently, within the preceding 10–15 years, judging by the size of the small trees, and

it appeared to have been caused by water-saturated earth slumping from a particularly steep portion of the slope. The seep was still visible and was in fact so wet that *Typha* bulrushes were found growing at the base of the slide. The area was characterized by pioneer species such as the fern *Dicranopteris linearis* and trees *Dombeya*, *Croton*, *Weinmannia*, and *Maesa*. The drier habitats, found on the thinner soils with underlying rock, were characterized by a species of *Philippia* and a tall *Helichrysum*. *Nastus* was common along the forest/landslide boundary.

1200 m

This altitudinal zone was located on a narrow ridge that was reached by climbing a steep trail up from the Andranohela River. Being on a ridge, both groundwater and large boulders were much rarer than at the lower sites. Much of the ground was covered by a spongy carpet of moss and fine



FIG. 2-4. View from edge of steep slope at about 1200 m in parcel 1 of the RNI d'Andohahela. Evening mist was a regular occurrence in this zone and at higher elevations, related to increased epiphyte cover (50–80%), mostly mosses and lichens. Lianas were still present in certain areas, but they were on average less common than at lower elevations. The understory was relatively open and usually consisted of Acanthaceae, young saplings of canopy species, and some *Oncostemum*, *Cyathea*, and *Marattia fraxinea* in the moister areas. (Photograph by N. Helme.)

root material that was to occur from this zone on up to the summit. The underlying dry soil was not sandy and turned quickly to dust by the passing of many feet.

A major structural change occurred progressively between 1000 and 1200 m, highlighting the shift from lowland to moist montane forest. Probably the most obvious change was an increase in tree density, with 50% more stems in our 1 ha plot than in those plots at 440 and 840 m (Chapter 4, Table 4-1). Paralleling this increase in total stem number was a small decrease in mean stem diameter. The plot was dominated by Myrtaceae (*Syzygium* spp.), with other important families being Lauraceae (*Cryptocarya*, *Ocotea*), Sterculiaceae (*Dombeya*), Moraceae, and Monimiaceae (*Tambourissa*). This high density of trees was repeated in our plot at 1950 m, where Lauraceae was once again dominant. This was the only elevation at which large palms (*Ravenia* sp.) formed a significant part of the canopy. Canopy height varied from 12 to 20 m, and there were no

clear emergents. *Sloanea rhodantha* was still present, but perhaps because of its lesser average height at this elevation, it did not have the enormous buttress roots so characteristic of this species at lower elevations. *Dilobeia thouarsii* dropped out completely by 1000 m, but *Canarium boivini* was still present in small numbers. Other large canopy elements included the predominantly lowland *Chrysophyllum boivianum* and the widespread *Croton monge*.

Evening mist was a feature of the forest at 1200 m and above; this was reflected in the substantial increase in epiphyte loads (Fig. 2-4). The majority of the epiphyte community consisted of mosses and lichens (50–80% cover), with ferns (especially *Hymenophyllum* and *Asplenium* spp.) making up a smaller component. Epiphytic orchids (*Bulbophyllum* spp.), melastomes (*Medinilla* sp.), *Rhipsalis baccifera*, and *Peperomia* spp. were present in low numbers. Lianas were still common in certain areas, but they were on average less common than at lower elevations. The understory

was relatively open and usually consisted of Acanthaceae, young saplings of canopy species, some *Oncostemum* spp., and the ferns *Cyathea* spp. and *Marattia fraxinea* in the moister areas.

The forest along the ridge leading up to the higher zones of the massif was structurally and floristically very different from the forest on the small plateau above the 1200 m site. The ridge had thin soils and was exposed to strong winds and rapid changes in humidity, with the result that the canopy was seldom above 8 m and trunks were often twisted and densely packed. Prominent trees included *Brachylaena*, *Weinmannia* spp., *Symphonia*, *Anthocleista*, *Syzygium* spp., *Macaranga*, and various Lauraceae, Rubiaceae, and Araliaceae. The epiphyte load was heavy. The understory was often dominated by a species of *Arundinaria* bamboo that grew to 2 m and appeared to have an inhibiting influence on the regeneration of other small plants. The lianescent bamboo *Nastus* was also present on the ridge, but it seldom dominated. At various points along the ridge were prominent granite outcrops, and on these grew another, larger species of bamboo (*Arundinaria* sp.) with irritating hairs on the culm leaves. This species was common within the 1875 m elevational zone in similar rocky habitats.

1500 m

The trail between the 1200 m and 1500 m zones followed the ridge leading up to Pic Trafonaomby and passed through the stunted ridge forest with its bamboo understory. The 1500 m site was situated in a large bowl (virtually a hanging valley) to the southeast of the peak. This bowl was drained by a number of small streams that came together just below the camp to form one of the main tributaries of the Andranohela River. The soils in the area were deep, presumably having accumulated from centuries of erosion of the surrounding slopes, and large boulders had also come to rest in the valley.

The forest in the valley was classified as mid-altitude montane forest (Humbert & Cours Darne, 1965), while the forest on the ridges had distinctly sclerophyllous characteristics typical of more exposed situations. The trees in the valley bottom, dominated by *Sloanea rhodantha* var. *rhodantha* form *quadriloba*, were exceptionally large, often attaining a height of 25 m, an extremely unusual situation at this altitude. The deep soils and abundant water in the valley may partially explain this

unexpected vigor. *Strongylodon* lianas were abundant and often attained a great size in the valley habitat, but they quickly disappeared on the thinner ridge soils, as did *Sloanea*. The slopes immediately above the *Sloanea* zone, at the base of the ridge, were dominated by *Ravensara* and a large species of *Tambourissa*. A highly characteristic tree at this elevation was the narrow-leaved *Pandanus vandamii*, a common canopy element in both valleys and on ridges; this species also occurs in the Western Domain. Large tree ferns (*Cyathea* spp.) were also a typical feature in this area, indicating the permanently moist nature of the site.

Notable by its absence was *Podocarpus madagascariensis*, not recorded anywhere on the massif but previously reported from Beampigaratra, Mandena, and Mahatalaky and known from littoral zones up to 1800 m (Koechlin et al., 1974). The apparent absence of this genus in the RNI d'Andohahela is in striking contrast to the RNI d'Andringitra, where it was the second most common tree at 1600 m (Lewis et al., 1996). Other notable absences (all common at lower elevations) included the dwarf *Dypsis* palms, the 7-m-tall *Dypsis scottiana*, *Diospyros* spp., Moraceae, and the large tree *Chrysophyllum boivinianum*.

Large areas in the valley were dominated by the climbing bamboo *Arundinaria*, which forms dense stands about 5 m above the ground. Scattered large trees can be found in these bamboo patches, rising up above the smothering layer, suggesting that the bamboo has only recently colonized the immediate area. Had the bamboo been there for a long time it is unlikely that the saplings would have survived in the light-starved environment below. This then begs the question as to just what caused the bamboo invasion. One possible scenario is that there was a tree fall, and the bamboo was able to take advantage of this light gap to colonize the immediate surroundings, outcompeting other species and gradually coming to dominate the understory. The bamboo will at some stage flower and die, and forest dynamics will then once again determine whether it is bamboo or woody species that fill the gap. It is difficult to speculate about such vegetation patterns when they are viewed through such a small window of time.

Certain areas along the ridge, up to 1750 m, had a dense understory of the same 2-m-tall *Nastus* bamboo. The moister areas in the valley were often dominated by extremely dense populations of a 1.8-m-tall *Impatiens*, particularly in light

gaps, while the slightly better drained areas supported the monocarpic *Ruellia*, *Gravesia dichaeanthoides*, *Vernonia leandrii*, *Blechnum* ferns, and *Laportea meddellii*. Common understory shrubs included *Pleuridantha liallyii*, *Filicium*, *Aphloia*, and *Oncostemum* spp. There were some large clearings (0.5 ha) in the forest, perhaps caused by cyclone-generated windthrow, that were invaded by various leguminous plants, *Urticaceae*, *Acanthaceae*, and *Balsaminaceae*, and by pioneer tree species such as *Macaranga* and *Dombeya*. The reason why bamboos were dominant in some areas and absent in other areas is not known.

Epiphytes were predictably abundant, with 80–100% cover on most horizontal branches. Orchids were no longer dominated by *Bulbophyllum*, and they included numerous small species. The unusual and attractive liliaceous epiphyte *Rhodocodon urGINEOIDES*, with small white flowers, was common on the trunks of *Sloanea* and other rough-barked species, and it appeared to be restricted to this elevation. The pink-flowered *Bakerella clavata* was a common branch parasite, as it was throughout the altitudinal range from 400 to 1800 m, but it was joined by a yellow-flowered form of *B. clavata* at the higher elevations (>1600 m).

The forest on the ridges was composed of small-leaved, twisted trees 8–10 m tall, a growth form molded by the strong winds that are a feature of this habitat. Mosses and lichens covered the trees and created a deep, spongy carpet on the ground. Typical canopy species included *Dicoryphe viticoides*, *Tina isoneura*, *Elaeocarpus* sp., *Gaertnera* sp., *Agauria* sp., *Anthocleista* sp., *Dombeya subsquamosae*, *Ehippiandra* sp., and *Weinmannia* sp.

1875 m

Our highest study elevation was located on the northern slopes of Andohahela Massif, due north of Pic Trafonaomby. After leaving the 1600 m site we passed through humid montane forest and, near the summit, into a zone of moss and bamboo with a high proportion of exposed rock. At 1875 m the bamboo gave way to a peculiar 8-m-tall montane forest (*sensu* Humbert & Cours Darne, 1965) with an open understory consisting almost entirely of a single species of sedge, *Apodocephala pauciflora*. As we descended the northern side of the peak the terrain once again became rocky, and the sedge rapidly disappeared. A small plateau sloped gently down toward the north before

becoming steeper at about 1800 m, and this area of deeper soils was characterized by a dense understory of *Acanthaceae*, with a few specimens of *Gesneriaceae* and a humid montane forest canopy of 6–10 m (Fig. 2-5). Secondary grasslands and burnt mid-altitude forest marked the northern boundary of the pristine forest. These short grasslands and remnant forests form a mosaic that is constantly changing according to the patterns of encroaching man-made fires that may scour the area in the dry season. Some large patches (>100 ha) of remnant forest on these northern slopes between 1400 and 1800 m are still connected by viable forest corridors. Below about 1300 m on the northern slopes the mid-altitude forests end abruptly and give way to secondary grasslands. Still lower, patches of dry forest indicate the beginning of the transitional zone between humid and spiny bush forest.

Because trees extend right to the top of the mountain, there is no real tree line as there is on certain of the higher peaks in Madagascar. Where trees are not present (mainly on rocky outcrops), having been replaced by shrubs and grasses, this is due to soil depth rather than the effects of altitude. The most extreme form of the stunted sclerophyllous forest is, not surprisingly, found on the summit of Pic Trafonaomby (1959 m) itself. The peak is a small granite outcrop, partly covered in sclerophyllous forest on the thin soils, with shrubs and succulents on the rock. The canopy was no more than 3 m tall and consisted of *Philippia* spp., *Alberta*, *Pittosporum*, *Agauria*, *Vaccinium*, and *Dombeya seyrigii*. The ground was covered by a thick mat of moss and *Lycopodium*, as is common in much of the area above 1800 m. Exposed rock near the summit supported a large *Aloe humbertii*, numerous *Helichrysum* spp., a sedge *Kyllinga plurifoliata*, and the herbaceous *Kniphofia ankarandensis*. The epiphyte load was heavy, with most tree limbs being densely clothed in moss. Lianas were virtually absent.

The 1 ha plot was located at 1950 m on the deep soil plateau with an *Acanthaceae* understory, just below and to the north of the peak. Although there was a high stem density, species diversity was low, and the area was dominated by the families *Araliaceae* (three species), *Lauraceae* (seven species), *Myrtaceae* (seven species), *Clusiaceae* (one species), and *Flacourtiaceae* (two species). No palms were recorded within the 1875 m zone, the highest elevational record being scattered *Dypsis* individuals at 1600 m (both north and south slopes).



FIG. 2-5. View of humid montane forest at 1875 m on plateau below Pic Trafonaomby in parcel 1 of the RNI d'Andohahela. This is the site of the fifth 1 ha plot (see Chapter 4). The forest, with a canopy of 6–10 m, was on a deep soil plateau and characterized by a high stem density with low species diversity, dominated by the families Araliaceae, Lauraceae, Myrtaceae, Clusiaceae, and Flacourtiaceae. The dense understory was made up of Acanthaceae and a few specimens of Gesneriaceae. (Photograph by N. Messmer.)

Our camp was located in a valley at about 1700 m, in a patch of mid-altitude montane forest that had been severely degraded by cattle trampling and grazing. The forest patch was separated from the main forest to the south by a band of secondary grassland approximately 300–900 m wide. *Smilax* was a common climber in these disturbed forests, and the 6–10-m-tall canopy was composed of *Tina*, *Philippia*, *Cephalostachyum* and *Nastus* bamboos, *Cassinopsis madagascariensis*, and a *Weinmannia* sp. The forest margin was made up of a predictable community of shrubs consisting largely of *Philippia*, together with *Vaccinium* and various Asteraceae, such as *Brachylaena merana*.

The grassland in the vicinity of our camp contained a number of species not found elsewhere on the expedition, such as the attractive Gesneriaceae *Tchiadenus longiflorus*, a shrubby umbellifer *Helichrysum* spp., a spiny *Mimosa dasyphylla*, and numerous sedges and grasses (*Sporobolus centrifugus*, *Bulbostylis hispidula*, and *Eleocharis*

limosa). It is not known whether any of this short grassland is natural (it is short largely because of cattle grazing) or whether it is all secondary, the result of repeated burning of the forest and cattle damage. It is suspected that small areas of natural grassland probably existed around the exposed and highly weathered granite domes in the area, where the soils are too thin to support a forest, although the species present now are not necessarily members of the original suite. Supporting evidence comes from a large dome to the east of camp that had apparently never been burned (judging by the surrounding forest and because its steep slopes made it unsuitable for cattle). This large area had few species in common with the grasslands around camp, although the life forms were similar, including various abundant sedges (*Costularia baroni*), a grass (*Danthonia macowanii*), *Myrica phillyreaefolia* shrubs, *Viscum tieghemii*, and scattered *Philippia* spp. Poor drainage on the shallow soils is further indicated by *Sphagnum* moss and the fern *Blechnum tabulare*.



FIG. 2-6. View of the descent along the western slopes of the Anosyenne Mountains toward Esomony at about 1650 m. The lower limit of the forest was created by human disturbance, largely fire, and the lower grasslands are virtually treeless. The few trees present are scattered *Brachylaena* and *Agauria*. At about 900 m the first *Kalanchoe beharensis* and *Pachypodium lamerei* were noted, indicating the moist/dry forest ecotone. (Photograph by N. Helme.)

Pteridium aquilinum (bracken) was absent, suggesting that the area had not been seriously disturbed by man and supporting the idea that some sort of grassland may also have been the natural vegetation around the domes near camp.

An unusual habitat occurred on the northern slopes below camp, at about 1550 m, in an area known locally as Ankebotsy. The area was permanently moist, seasonally flooded, and had typical marsh vegetation, characterized by an absence of trees and an abundance of sedges. The 2 ha area had been badly overgrazed by cattle and burned too frequently, but it still supported some interesting species such as the lily *Kniphofia ankarendensis*, *Sphagnum* moss, an Eriocaulaceae, *Philippia*, and the fern *Osmunda regalis*.

From the 1700 m camp we descended on the footpath to the village of Esomony, located at the northwestern base of the Andohahela Massif. The lowest forest is at about 1300 m and is typical mid-montane forest, as found on the southeastern side of the mountain, although the local rainfall is almost certainly less. The lower limit of the

forest was created by fire, and the grassy slopes below are virtually treeless (Fig. 2-6). The few trees present are scattered *Brachylaena* and *Agauria*, the latter seemingly protected from the flames by its thick bark. In the moist ravines we found small groves dominated by a *Weinmannia*. At about 900 m we encountered the first *Kalanchoe beharensis* and *Pachypodium lamerei*, indicating that we had already crossed the moist/dry forest ecotone. Not much transitional or spiny forest remains in the area, and most of what can be seen is restricted to the steep, rocky outcrops. At about 700 m were small (approximately 5 ha) remnant forests dominated by the trees *Adansonia za* and *Alluaudia* spp., and the dramatic transition from humid montane forest to dry spiny forest was complete.

Spiny Forest at 120 m

Our final study site was located in parcel 2 of RNI d'Andohahela, some 50 km southwest of Pic



FIG. 2-7. View of the spiny forest of parcel 2 of the RNI d'Andohahela, some 50 km southwest of Pic Trafonaomby. The spiny forest is characterized by the dominance of the endemic family Didieraceae, particularly the lanky *Alluaudia procera* and *A. ascendens* in the central foreground, and a large number of *Euphorbia* species. (Photograph by N. Messmer.)

Trafonaomby. The area is within the spiny forest, also known as the Southern Domain, and is characterized by the dominance of the endemic family Didieraceae and a large number of *Euphorbia* species (Perrier de la Bâthie, 1921; Humbert, 1955). The vegetation is a thicket, at times even a forest, of drought-resistant species, many of them succulent (Fig. 2-7). The camp was located along a tributary of the Mananara River, about 7.5 km east of the village of Hazofotsy. Small granitic hills to the south provided a different, rockier habitat than the predominant plains with their sandy soils. These sands are often merely derived from the weathered granite, but there are also patches of deep, red, Pliocene sands. Small outcrops of hard, white calcrete are occasionally visible. Much of the immediate surrounding forest has been selectively logged. The gallery forest along the Mananara has been severely degraded, but there are still examples of deciduous forests, dominated by *Tamarindus indica*, in certain areas.

Structurally the spiny forest is fairly homogeneous, with similar tree densities recorded in a wide range of microhabitats, from sandy valleys

to rocky hills. Probably the most characteristic taxa were the lanky *Alluaudia procera* and *A. ascendens*, species that may form a 15-m-tall forest. These trees may be thought of as emergents because they are about 5 m taller than most other species. Burseraceae was well represented by at least five species of *Commiphora*, while *Euphorbia* formed a co-dominant in the canopy, with five species recorded in the area.

Other common trees included *Gyrocarpus americanus*, *Cedrelopsis grevei*, *Boscia longifolia*, *Operculicarya decaryi*, *Tetrapterocarpon geayi*, *Grewia* spp., *Strychnos* spp., *Fernandoa*, *Stereospermum*, *Diospyros* sp., *Hazunia modesta*, *Croton* spp., and *Obetia* sp. Baobabs were represented by *Adansonia za*, some of them reaching a diameter of 5 m, but they were not particularly common. Palms and bamboos were entirely absent.

There was an obvious shrub layer about 1–3 m high. This layer was dominated by *Dichrostachys decaryana* in the disturbed areas, where it was often quite dense. The understory was relatively open in the less disturbed areas and was com-

posed of species such as *Rhigozum*, various Acanthaceae, *Bauhinia* sp., *Koehnaria madagascariensis*, *Grewia* spp., *Aloe vaombe* and *A. divaricata*, *Croton* spp., *Hibiscus* spp. and other Malvaceae, and various Fabaceae. Terrestrial grasses were uncommon and seldom made up a significant portion of the ground cover. By far the most important component in the ground cover category was a small and extremely drought-tolerant fern—*Selaginella* spp. (see Chapter 3). This plant covered large areas, turning green for a few days after a rainfall event but soon reverting to its usual gray, desiccated state.

Lianas were present but were usually small and dominated by species of Asclepiadaceae, Apocynaceae, and Cucurbitaceae. Epiphytes were predictably rare in such a dry environment, the best represented being foliose lichens. A single species of epiphytic orchid (*Angraecum*) was found. Noticeably absent were the branch parasites *Viscum* and *Bakerella* and the epiphytic Cactaceae *Rhipsalis baccifera*.

The riverine area supported not only large *Tamarindus indica* trees, but a number of *Ficus* spp. (including *F. marmorata*), large beds of *Phragmites* reed, shrubs such as *Phyllanthus*, and various weedy Cyperaceae and Juncaceae. A potential threat to the forest in certain areas were dense infestations of the highly invasive vine *Cissus quadrangulare*. This plant forms a smothering blanket over all existing vegetation and is capable of severely altering the habitat if not controlled.

The rocky hills provided a different habitat, with shallow soils and a change in aspect. The vegetation most characteristic of these hills were the northeast-facing colonies of *Pachypodium lamerei*, a 3 m, extremely spiny pachycaul shrub. Trees such as *Tetrapterocarpon geayi* were replaced by *Melia azedarach*, and *Uncarina* sp. became more common.

The calcrete outcrops had a slightly impoverished flora dominated by the spiny shrub *Euphorbia stenoclada*, a species renowned for forming impenetrable thickets in such habitats further south and along the southern coast.

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Chapter 3

Pteridophytes of the Eastern Slope of the Réserve Naturelle Intégrale d'Andohahela, Madagascar: Distribution and Floristic Analysis

France Rakotondrainibe¹

Abstract

The pteridophyte flora of the eastern slope of the Réserve Naturelle Intégrale (RNI) d'Andohahela (parcel 1) comprises 207 species and varieties in 69 genera. One as yet undescribed species of *Xiphopteris* is currently considered endemic to the massif, and three other species are regional endemics.

Data collected from 18 plots, covering a surface area of 13,600 m² and containing 162 species, were subjected to an ascending hierarchical classification and a principal components analysis. Altitude accounted for 55.5% of the floristic heterogeneity among the plots. Based on floristic composition of the ferns, four altitudinal stages can be recognized between 400 m and 1956 m on the eastern slope. Each of these stages is characterized with regard to the physiognomy of its vegetation and various aspects of the pteridophytes present, including the range of growth forms, generic and specific composition, average species density, and the presence of species that are exclusive to a stage or exhibit a strong preference.

Comparison of the pteridophyte flora of the RNI d'Andohahela with that of the Réserve Spéciale d'Anjanaharibe-Sud, located in extreme northern Madagascar within the same bioclimatic zone but nearly 10° of latitude closer to the equator, shows a striking floristic similarity in the lower altitudinal strata, and equally strong differences above 1500 m.

Résumé

La flore ptéridologique du versant est de la Réserve Naturelle Intégrale (RNI) d'Andohahela (parcelle 1) comprend 207 espèces et variétés réparties en 69 genres. L'une d'elle, non encore décrite, appartenant au genre *Xiphopteris*, est considérée à l'heure actuelle comme endémique du massif et 3 autres sont des endémiques régionales.

Les données recueillies sur 18 parcelles totalisant une superficie de 13.600 m² et concernant 162 espèces, ont été soumises à une classification ascendante hiérarchique et à une analyse factorielle des correspondances. Le facteur altitudinal rend compte de 55,5% de l'hétérogénéité floristique des parcelles. Sur la base de leur composition floristique en Ptéridophytes, quatre étages altitudinaux ont été reconnus sur le versant est, entre 400 et 1957 m. Pour chacun d'eux nous précisons la physiognomie de la végétation et les caractéristiques du peuplement des Ptéridophytes, à savoir: le spectre des types biologiques, la composition générique et spécifique, la densité spécifique moyenne, les espèces caractéristiques exclusives et préférentielles.

La comparaison de la flore ptéridologique de la RNI d'Andohahela avec celle de la Réserve Spéciale d'Anjanaharibe-Sud situé à l'extrémité nord de Madagascar, dans la même zone bio-

¹ Laboratoire de Phytomorphologie, Ecole Pratique des Hautes Etudes, 16, rue de Buffon, 75005 Paris, France.

climatique mais à une latitude inférieure de 10°, met en évidence des ressemblances floristiques frappantes dans les strates altitudinales inférieures et au contraire des différences tout aussi remarquables à partir de 1.150 m d'altitude.

Introduction

Parcel 1 of the Réserve Naturelle Intégrale (RNI) d'Andohahela is located in extreme south-eastern Madagascar, in the Anosyenne Mountains (see Chapter 1). The information presented in this chapter was gathered in the northern part of the reserve, and specifically in the watershed of the Andranohela River as well as its headwaters on the slopes below the Trafonaomby Massif. This ancient granitic and gneissic massif culminates at 1956 m.

Since Humbert (1941) published his overview of the Andohahela area, very little work has been published on the vascular plant flora of the area, despite the increasing number of botanists who have visited the reserve. Careful study of the herbarium material collected in 1928 and 1933–1934 by Humbert in the three massifs of the Anosy Range that are the closest areas to the study site (Pic Varavara, Pic Trafonaomby, and Pic Andohahela) resulted in a list of 28 species or varieties of pteridophytes, only five of which came from the eastern slope of Trafonaomby. Based on existing collections and literature it is clear that the fern flora of the RNI d'Andohahela is among the most poorly known in Madagascar.

The aims of this chapter are to (1) present an inventory of the pteridophytes occurring on the eastern slope of the RNI d'Andohahela, (2) describe the patterns of distribution of the taxa, and (3) compare the results of the present study conducted in the southern part of Madagascar with a similar study conducted in the extreme northern part of the island, in the Réserve Spéciale (RS) d'Anjanaharibe-Sud (Rakotondrainibe & Rahari-malala, 1998).

Study Area: Climatic Stages and Vegetation

The Andranohela Basin is situated in the humid climatic stages, characterized by average annual minimum temperatures between 10° and 13°C and a water deficit of less than 100 mm (Cornet, 1974). The eastern slope of the RNI d'Andohahela, between about 600 and 800 m,

falls within the subhumid stage, characterized by a dry season that is attenuated by mist and fog, temperatures between 7° and 10°C, and a water deficit of less than 200 mm. The summit area, for which no climatological data are available, is placed by Cornet (1974) in his montane stage, with temperatures less than 5°C, and specifically within a humid subset with no dry season.

The entire study area is covered by dense moist evergreen forest, the physiognomy of which changes progressively with increasing altitude. As elsewhere in Madagascar, the following vegetation types can be recognized (Guillaumet & Koechlin, 1971; Paulian et al., 1973; Cornet & Guillaumet, 1976; F. Rakotondrainibe, pers. observ.): (1) low-elevation dense evergreen forest, with a canopy reaching 20–30 m in height, trunks that are straight and free of epiphytic mosses, almost no herbaceous ground cover, and large-diameter lianas that are abundant within the canopy and the understory; (2) montane dense evergreen forest with a canopy rarely exceeding 20 m in height, an herbaceous ground cover that is open to very dense, abundant mosses on the trunks, and many small-diameter lianas; and (3) dense sclerophyllous montane forest near the summit, on ridges, and in areas with shallow soil, comprising trees 8–12 m tall, with twisted branches and trunks that are often declining or prostrate, with a thick carpet of mosses on the ground and the bases of the trees.

Montane thicket vegetation, a low, very dense ericoid formation characteristic of the highest summits, does not occur on Pic Trafonaomby. The transition between low-elevation evergreen forest of the Eastern Domain and the mid-elevation forest in the Central Domain usually occurs at around 800 m (Perrier de la Bâthie, 1921), but in the extreme southern part of Madagascar the transition is found at about 600 m (Humbert, 1935).

Methodology

The present study was conducted using the same methodology described earlier for inventory work performed in 1994 in the RS d'Anjanaharibe-

Sud (Rakotondrainibe & Raharimalala, 1998) and in 1993 in the RNI d'Andringitra (Rakotondrainibe & Raharimalala, 1996).

Floristic Survey

The floristic inventory was carried out within a 2 km radius around five camps, i.e., between 420 and 550 m (camp 1), 750 and 850 m (camp 2), 1150 and 1280 m (camp 3), 1470 and 1570 m (camp 4), and 1850 and 1956 m (camp 5). The data were supplemented by observations and collections made along the main trail connecting the camps that runs from the village of Enosiary to Pic Trafonaomby, following the ridge lines above the left bank of the Andranohela River (see Chapter 1).

All voucher specimens were deposited in the herbarium of the Département des Recherches Forestières et Piscicoles, Centre National de la Recherche Appliquée au Développement (DRFP/FOFIFA), in Antananarivo (TEF), and the Laboratoire de Phanérogamie, Muséum National d'Histoire Naturelle, in Paris (P). Duplicates of most of the species collected will be sent to the Missouri Botanical Garden, St. Louis (MO) and the Royal Botanic Gardens, Kew (K).

In most cases, generic delimitations have followed those proposed by Kramer and Green (1990), although for certain genera whose circumscription is controversial and which are in need of revision, particularly for the Malagasy flora, more classic concepts have been used: Grammitidaceae follows Pichi-Sermolli (1977) and Thelypteridaceae uses the system of Holttum (1974). *Megalastrum* (Dryopteridaceae) is treated as a separate genus, as suggested by Holttum (1986). The determination of species and varieties was made using Malagasy and African flora treatments (Christensen, 1932; Tardieu-Blot, 1951–1971; Schelpe, 1970; Schelpe & Anthony, 1986) and monographs of *Lastreopsis* genus (Tindale, 1965), Lindsaeaceae family (Kramer, 1972), and Thelypteridaceae family (Holttum, 1974).

All of the data presented here concern the pteridophytes that occur in moist forest within parcel 1 of the RNI d'Andohahela. Information on a few ferns observed in the spiny forest of parcel 2 is given in Appendix 3-1.

Ecological Sampling

In order to characterize the pteridophyte associations in the different biotopes within the study

area and to assess the ecological factor(s) responsible for patterns of distribution among the taxa represented, data were collected from plots. As far as possible one plot was established in each biotope such that when taken together, they afforded a representative sample of the study area. Thus, 18 ecological plots were established, 14 on slopes (P1–P14) and four along watercourses (R1–R4). Tables 3-2 and 3-3 summarize the physical, topographic, and biological features of the plots. The minimal area needed for a representative sample of pteridophytes in humid forest in Madagascar is between 500 and 1,000 m², depending on the diversity of the biotope (Rakotondrainibe & Raharimalala, 1998). The area of each plot in this study is 800 m², except for plot P11 (400 m²), established on a narrow ridge. Each plot consisted of eight subunits of 100 m², the arrangement of which depended on the topography. The number of species present in each plot as a percentage of the total fern flora identified from the general inventory in each area provides an indication of how representative they are, with values ranging from 67.9% to 84.0% and averaging 78.3% (which corresponds to 162 taxa present in the plots out of a total of 207 identified from the study area). The lowest value (67.9%) was obtained near the summit, where time constraints made it impossible to sample the vegetation in two areas, a nonforest swamp and a large stone slab. The swamp and stone slab clearly had a low number of highly specialized species that could thus be described adequately without having to use quantitative methods. Considering that most tropical formations have a rather large number of infrequently encountered species, the average value of 78.3% is considered sufficient to indicate that the floristic composition of the study plots adequately represented that of the surrounding vegetation.

The methods used for the plot analyses (choice of site, size of plots, and procedures for data collection) have been described elsewhere (Rakotondrainibe & Raharimalala, 1998). To facilitate interpretation of the results presented here, however, we briefly discuss types of field observations and how they were recorded. The following were recorded for each plot:

- A. A complete list of species encountered.
- B. The number of individuals or colonies of each species, coded by abundance class, according to the following categories:
 - 1. 1 individual or colony
 - 2. 2–4 individuals or colonies

TABLE 3-1. Pteridophytes of the eastern slope of the RNI d'Andohahela (parcel 1): Floristic composition, habit type, and altitudinal distribution.

No.	Taxa*	420– 550 m	810– 1150 m	1280– 1500 m	1510– 1957 m	Habit type
1	<i>Adiantum madagascariense</i> H. Rodend. var. prolongatum (Bonap.) Tardieu	+	–	–	–	T
2	<i>Adiantum phanerophlebium</i> (Baker) C. Chr.	+	–	–	–	T
3	<i>Amauropelta bergiana</i> (Schltdl.) Holttum	–	–	+	+	T/r
4	<i>Angiopteris madagascariensis</i> de Vriese	+	–	–	–	T
5	<i>Antrophyum bivittatum</i> C. Chr.	–	–	–	+	E
6	<i>Antrophyum boryanum</i> (Willd.) Kaulf.	–	–	+	–	E/r
7	<i>Antrophyum malgassicum</i> C. Chr.	+	+	–	–	E/r
8	<i>Arthropteris monocarpa</i> (H. L. Cordem.) C. Chr.	+	+	+	+	E/r
9	<i>Arthropteris orientalis</i> (J. F. Gmel.) Posth. var. <i>subbiaurita</i> (Hook.) C. Chr.	+	+	–	–	T/E
10	<i>Asplenium aethiopicum</i> (Burm.) Bech.	–	+	+	+	E/r
11	<i>Asplenium auritum</i> Sw.	–	+	–	–	E/r
12	<i>Asplenium bipartitum</i> Bory	+	–	–	–	E/r
13	<i>Asplenium blastophorum</i> Hieron.	+	+	–	–	T/E/r
14	<i>Asplenium cuneatum</i> Lam.	+	+	–	–	E/r
15	<i>Asplenium dregeanum</i> Kunze	–	+	–	–	R
16	<i>Asplenium erectum</i> Bory ex Willd. var. <i>erectum</i>	–	+	+	+	T/r
17	<i>Asplenium erectum</i> Bory ex Willd. var. <i>zeyheri</i> (Pappe & Rawson) Alston & Schelpe	–	+	+	–	T/r
18	<i>Asplenium friesianum</i> C. Chr.	–	+	+	+	T/E/r
19	<i>Asplenium herpetopteris</i> Baker var. <i>herpetopteris</i>	+	+	+	–	E/r
20	<i>Asplenium herpetopteris</i> Baker var. <i>massoulae</i> (Bonap.) Tardieu	–	–	+	–	E/r
21	<i>Asplenium inaequilaterale</i> Willd.	+	+	–	–	T/r
22	<i>Asplenium lividum</i> Mett. ex Kuhn	–	+	–	–	E
23	<i>Asplenium mannii</i> Hook.	–	+	+	+	E
24	<i>Asplenium nidus</i> L.	+	+	–	–	E/r
25	<i>Asplenium normale</i> D. Don	–	+	+	+	T/r
26	<i>Asplenium pellucidum</i> Lam.	+	+	–	–	E/r
27	<i>Asplenium petiolulatum</i> Mett.	–	+	+	+	E
28	<i>Asplenium poolii</i> Baker var. <i>poolii</i>	–	+	+	+	T/E/r
29	<i>Asplenium poolii</i> Baker var. <i>linearipinnatum</i> (Bonap.) C. Chr.	–	+	–	–	T/r
30	<i>Asplenium prionites</i> Kunze	–	+	–	–	E
31	<i>Asplenium protensum</i> Schrad.	–	–	+	+	E/r
32	<i>Asplenium rutifolium</i> (P. J. Bergius) Kunze	–	+	+	+	E
33	<i>Asplenium sandersonii</i> Hook.	+	+	+	+	T/E/r
34	<i>Asplenium theciferum</i> Kunth	–	+	–	+	E/r
35	<i>Asplenium thunbergii</i> Kunze	+	+	+	+	T/E/r
36	<i>Asplenium unilaterale</i> Lam.	+	–	–	–	T/r
37	<i>Asplenium variabile</i> Hook. var. <i>paucijugum</i> (Ballard) Alston	+	–	–	–	T/E/r
38	<i>Asplenium virchowii</i> Kuhn	–	+	–	–	R
39	<i>Asplenium viviparioides</i> Kuhn	–	–	–	+	T
40	<i>Athyrium scandicinum</i> (Willd.) C. Presl	–	–	+	–	T
41	<i>Belvisia spicata</i> Mirbel	–	+	+	–	E
42	<i>Blechnum attenuatum</i> (Sw.) Mett.	+	+	+	–	T/E/r
43	<i>Blechnum attenuatum</i> (Sw.) Mett. var. <i>giganteum</i> (Kaulf.) Bonap.	–	–	+	–	T
44	<i>Blechnum bakeri</i> (Baker) C. Chr.	–	–	+	–	T
45	<i>Blechnum ivohibense</i> C. Chr.	–	+	+	–	T
46	<i>Blechnum madagascariense</i> Tardieu	–	–	+	–	T
47	<i>Blechnum punctulatum</i> Sw.	–	–	–	+	T
48	<i>Blechnum simillimum</i> (Baker) Diels	–	+	+	–	T/E
49	<i>Blechnum tabulare</i> (Thunb.) Kuhn	–	–	–	+	T
50	<i>Blotiella pubescens</i> (Kaulf.) Tryon	+	+	+	–	T
51	<i>Christella dentata</i> (Forssk.) Holttum	+	–	–	–	T
52	<i>Christella distans</i> (Hook.) Holttum	+	+	–	–	T

TABLE 3-1. *Continued.*

No.	Taxa*	420- 550 m	810- 150 m	1280- 1500 m	1510- 1957 m	Habit type
53	<i>Christella multifrons</i> (C. Chr.) Holttum	+	-	-	-	T
54	<i>Cochlidium serrulatum</i> (Sw.) L. E. Bishop	-	+	-	-	R
55	<i>Coniogramme madagascariensis</i> C. Chr.	-	+	+	-	T
56	<i>Ctenitis cirrhosa</i> (Schumach.) Ching	+	-	-	-	T
57	<i>Ctenitis crinita</i> (Poir.) Tardieu var.? (FR 2869, 2884)	+	-	-	-	T
58	<i>Ctenitis madagascariensis</i> Tardieu	-	+	-	-	T
59	<i>Ctenopteris devoluta</i> (Baker) Tardieu	-	+	+	+	E
60	<i>Ctenopteris elastica</i> (Bory) Copel	+	+	-	-	E
61	<i>Ctenopteris flabelliformis</i> (Poir.) I. Sm.	-	-	-	+	T/E
62	<i>Ctenopteris villosissima</i> (Hook.) Harley	-	+	+	+	E
63	<i>Ctenopteris zenkeri</i> (Hieron.) Tardieu	+	+	-	-	E
64	<i>Cyathea</i> aff. <i>boivinii</i> Mett. (FR 2880, 2881, 3016)	+	+	-	-	T
65	<i>Cyathea</i> aff. <i>dregei</i> Kunze (FR 3136, 3234, 3122)	-	-	+	-	T
66	<i>Cyathea andohahelensis</i> (Tardieu) (= <i>Alsophila andohahelensis</i> Tardieu)	-	-	+	+	T
67	<i>Cyathea</i> aff. <i>bellisquamata</i> Bonap. (FR 3059)	-	-	+	-	T
68	<i>Cyathea borbonica</i> Desv. var. <i>laevigata</i> Bonap.	+	+	-	-	T
69	<i>Cyathea borbonica</i> Desv. var. 1 (FR 3150)	-	-	+	-	T
70	<i>Cyathea borbonica</i> Desv. var. 2 (FR 2968)	-	+	-	-	T
71	<i>Cyathea bullata</i> (Baker) Rakotondr.	-	+	+	-	T
72	<i>Cyathea costularis</i> Bonap.	+	+	-	-	T
73	<i>Cyathea decrescens</i> Mett.	-	+	+	-	T
74	<i>Cyathea melleri</i> (Baker) Domin	-	+	+	+	T
75	<i>Cyathea pilosula</i> Tardieu	-	+	-	-	T
76	<i>Cyathea</i> sp. 2 (groupe <i>C. borbonica</i>) (FR 3165)	-	-	+	-	T
77	<i>Cyathea tsilotsilensis</i> Tardieu	+	+	-	-	T
78	<i>Cyclosorus interruptus</i> (Willd.) Kato	+	-	-	-	T
79	<i>Cyrtomium caryotideum</i> (Wal. ex Hook. & Grev.) C. Presl var. <i>micropterum</i> (Kunze) C. Chr.	-	-	-	+	T
80	<i>Davallia chaerophylloides</i> (Poir.) Steud.	+	-	-	-	E
81	<i>Deparia parvisora</i> (C. Chr.) Kato	-	+	+	-	T
82	<i>Dicranopteris linearis</i> (Burm.) Underw.	-	+	-	+	T
83	<i>Didymochlaena truncatula</i> (Sw.) J. Sm.	-	+	-	-	T
84	<i>Diplazium</i> aff. <i>zakamenense</i> (Tardieu) Rakotondr. (FR 3081)	-	+	+	-	T
85	<i>Doryopteris kitchingii</i> (Baker) Bonap.	-	-	-	+	R
86	<i>Drynaria willdenowii</i> (Bory) Moore	+	-	-	-	E
87	<i>Dryopteris mangindranensis</i> Tardieu	+	+	+	-	T/r
88	<i>Dryopteris manniana</i> (Hook.) Tardieu	-	-	+	-	T
89	<i>Dryopteris remotipinnula</i> Bonap.	-	+	+	+	T
90	<i>Elaphoglossum acrostichoides</i> (Hook. & Grev.) Schelpe	-	-	+	+	E
91	<i>Elaphoglossum</i> aff. <i>conforme</i> (Sw.) Schott. (FR 2909, 3107, 3175)	+	-	-	-	T
92	<i>Elaphoglossum</i> aff. <i>sieberi</i> (FR 2962, 2991, 3025, 3188)	-	+	+	-	E
93	<i>Elaphoglossum</i> aff. <i>stipitatum</i> (FR 2918)	+	-	-	-	R
94	<i>Elaphoglossum</i> aff. <i>subsessile</i> (Baker) C. Chr. (FR 3022, 3066)	-	+	+	+	E
95	<i>Elaphoglossum angulatum</i> (Blume) Moore	-	-	-	+	E
96	<i>Elaphoglossum aubertii</i> (Desv.) Moore	-	-	+	+	T/E
97	<i>Elaphoglossum coursii</i> Tardieu	-	-	-	+	T
98	<i>Elaphoglossum decaryanum</i> Tardieu	-	-	+	+	E
99	<i>Elaphoglossum deckenii</i> (Kuhn) C. Chr. var. <i>rufidulum</i> (Willd.) Tardieu	-	-	+	+	E
100	<i>Elaphoglossum forsthii-majoris</i> H. Christ	-	+	-	-	E
101	<i>Elaphoglossum humbertii</i> C. Chr.	-	+	+	-	E
102	<i>Elaphoglossum hybridum</i> (Bory) Brack.	+	+	+	-	E/r

TABLE 3-1. *Continued.*

No.	Taxa*	420– 550 m	810– 1150 m	1280– 1500 m	1510– 1957 m	Habit type
103	<i>Elaphoglossum leucolepis</i> (Baker) Krajina var.? (FR 2990)	—	+	—	—	E
104	<i>Elaphoglossum petiolatum</i> ssp. <i>salicifolium</i> (Willd. ex Kaulf.) Schelpe	—	+	—	—	R
105	<i>Elaphoglossum poolii</i> (Baker) H. Christ	—	—	—	+	E
106	<i>Elaphoglossum pseudovillosum</i> Bonap.	—	+	—	—	E
107	<i>Elaphoglossum</i> sp. 9 (FR 3127)	—	—	+	+	E
108	<i>Elaphoglossum spathulatum</i> (Bory) Moore	+	+	—	—	R
109	<i>Elaphoglossum subsessile</i> (Willd.) C. Chr.	—	+	+	+	T
110	<i>Grammitis barbatula</i> (Baker) Copel.	—	—	—	+	E
111	<i>Grammitis cryptophlebia</i> (Baker) Copel.	—	—	+	+	R
112	<i>Grammitis gilpiniae</i> (Baker) Tardieu	—	—	+	—	R
113	<i>Grammitis holophlebia</i> (Baker) Copel.	—	—	+	+	E
114	<i>Grammitis microglossa</i> (C. Chr.) Ching	—	—	+	—	R
115	<i>Grammitis</i> sp. (FR 3197, 3230)	—	—	—	+	E
116	<i>Grammitis synsora</i> (Baker) Copel.	—	+	—	—	E
117	<i>Huperzia cavifolia</i> (C. Chr.) Tardieu	—	+	—	—	E
118	<i>Huperzia gagnepainiana</i> (Herter) Tardieu	—	—	+	—	E
119	<i>Huperzia humbertii-henrici</i> (Herter) Tardieu	—	—	+	+	E
120	<i>Huperzia megastachya</i> (Baker) Tardieu	—	+	—	—	E
121	<i>Huperzia obtusifolia</i> (Sw.) Rothm.	—	+	+	+	E
122	<i>Huperzia ophioglossoides</i> (Lam.) Rothm.	—	+	+	+	E
123	<i>Huperzia pecten</i> (Baker) Tardieu	—	+	+	+	E
124	<i>Huperzia squarrosa</i> (G. Forst) Trevis.	—	—	—	+	E
125	<i>Huperzia verticillata</i> (L. f.) Trevis.	—	+	+	+	E
126	<i>Hymenophyllum</i> aff. <i>fumarioides</i> Willd. (FR 3032, 3084, 3189)	—	+	+	+	E/r
127	<i>Hymenophyllum hirsutum</i> (L.) Swartz	+	+	+	+	E/r
128	<i>Hymenophyllum perrieri</i> Tardieu	—	+	+	+	E
129	<i>Hymenophyllum polyanthos</i> (Sw.) Sw.	—	+	+	+	E
130	<i>Hymenophyllum sibthorpioides</i> (Bory ex Willd.) Mett. ex Kuhn	+	+	+	+	E
131	<i>Hymenophyllum tunbrigense</i> (L.) Sm.	—	—	+	—	E
132	<i>Hymenophyllum veronicoides</i> C. Chr.	—	—	—	+	E
133	<i>Hymenophyllum viguieri</i> Tardieu	+	—	—	—	R
134	<i>Hypolepis sparsisora</i> (Schrader) Kuhn	—	+	—	—	T
135	<i>Lastreopsis pseudoperrieriana</i> (Tardieu) Tardieu	+	—	—	—	T
136	<i>Lepisorus excavatus</i> (Bory ex Willd.) Moore	—	+	+	+	E
137	<i>Lepisorus schraderi</i> (Mett.) Ching	—	—	—	+	E
138	<i>Lindsaea goudotiana</i> (Kunze) Mett. ex Kuhn	+	+	—	—	E
139	<i>Lindsaea madagascariensis</i> Baker	—	+	+	—	T
140	<i>Lomariopsis</i> aff. <i>crassifolia</i> (FR 2859, 3000)	+	+	+	—	R
141	<i>Lomariopsis</i> aff. <i>pollicina</i> Willem ex Kuhn (FR 2860)	+	+	—	—	E/r
142	<i>Loxogramme humblotii</i> C. Chr.	+	—	—	—	R
143	<i>Loxogramme lanceolata</i> (Sw.) C. Presl	+	+	+	+	E/r
144	<i>Lycopodiella caroliniana</i> (L.) Pic. Serm.	—	—	—	+	T
145	<i>Lycopodiella cernua</i> (L.) Pic. Serm.	—	+	—	—	T
146	<i>Lycopodium clavatum</i> L.	—	—	—	+	T
147	<i>Lygodium lanceolatum</i> Desv.	+	—	—	—	L
148	<i>Marattia fraxinea</i> Sm. ex J. F. Gmel.	+	+	+	—	T
149	<i>Megalastrum</i> aff. <i>magnum</i> (Baker) Holttum (FR 2874, 2934)	+	+	—	—	T
150	<i>Megalastrum lanuginosum</i> (Kaulf.) Holttum	+	—	+	—	T
151	<i>Microlepis madagascariensis</i> (Kunze) C. Presl	+	+	+	—	T
152	<i>Microlepis speluncae</i> (L.) Moore	—	—	—	—	T
153	<i>Microsorium pappei</i> (Mett.) Tardieu	—	+	—	—	R
154	<i>Microsorium punctatum</i> (L.) Copel.	+	+	—	—	E/r

TABLE 3-1. *Continued.*

No.	Taxa*	420- 550 m	810- 1150 m	1280- 1500 m	1510- 1957 m	Habit type
155	<i>Mohria caffrorum</i> (L.) Desv. = <i>M. marginata</i> J. P. Roux)	-	-	-	+	T
156	<i>Nephrolepis biserrata</i> (Sw.) Schott	+	+	-	-	T/E/r
157	<i>Nephrolepis tuberosa</i> (Bory) C. Presl	-	+	-	-	T/E
158	<i>Nothoperanema squamisetum</i> (Hook.) Ching	-	-	-	+	T
159	<i>Oleandra distenta</i> Kunze	+	+	+	-	E
160	<i>Osmunda regalis</i> L.	-	+	-	+	T
161	<i>Pellaea angulosa</i> (Bory) Baker	+	+	+	+	T
162	<i>Pellaea boivinii</i> Hook.	-	-	-	+	R
163	<i>Pellaea viridis</i> (Forssk.) Prantl var. <i>glauca</i> Sim.	-	+	-	+	R
164	<i>Phymatosorus scolopendria</i> (Burm.) Pic. Serm.	+	+	-	-	T/E/r
165	<i>Pityrogramma argentea</i> (Willd.) Domin	-	-	-	+	T
166	<i>Pityrogramma calomelanos</i> (L.) Link	+	-	-	-	R
167	<i>Pleopeltis macrocarpa</i> (Bory ex Willd.) Kaulf.	-	+	+	+	E/r
168	<i>Pneumatopteris remotipinna</i> (Bonap.) Holttum	-	+	-	-	T
169	<i>Pneumatopteris subpennigera</i> (C. Chr.) Holttum	-	+	+	-	T
170	<i>Polystichum coursii</i> Tardieu	+	+	+	+	T
171	<i>Pseudocyclosorus pulcher</i> (Bory ex Willd.) Holttum	-	+	-	-	T
172	<i>Pteridium aquilinum</i> (L.) Kuhn	-	-	-	+	T
173	<i>Pteris catoptera</i> Kunze	-	-	+	-	T
174	<i>Pteris elongatiloba</i> Bonap var. <i>remotivenia</i> Bonap.	-	+	-	-	T
175	<i>Pteris griseoviridis</i> C. Chr.	-	-	+	-	T
176	<i>Pteris pseudolonchitis</i> Bory	+	+	-	+	T
177	<i>Rumohra adiantiformis</i> (G. Forst.) Ching	-	+	+	+	T/E
178	<i>Rumohra</i> aff. <i>lokohoensis</i> Tardieu (FR 3033)	+	+	-	-	T/E
179	<i>Rumohra capuronii</i> Tardieu	-	-	+	-	E
180	<i>Saccoloma henriettae</i> (Baker) C. Chr.	-	-	+	-	T
181	<i>Schizaea dichotoma</i> L.	+	+	+	-	T
182	<i>Selaginella marinii</i> Stefanovic & Rakotondr.	-	+	-	-	R
183	<i>Selaginella pectinata</i> (Willd.) Spring	+	-	-	-	T
184	<i>Sphenomeris chinensis</i> (L.) Maxon	-	-	-	+	T
185	<i>Stenochlaena tenuifolia</i> (Desv.) Moore	+	-	-	-	T
186	<i>Sticherus flagellaris</i> (Bory) St. John	-	+	+	-	T
187	<i>Tectaria madagascariensis</i> Tardieu	+	+	-	-	T
188	<i>Thelypteris confluens</i> (Thunb.) C. V. Morton	-	+	-	-	T
189	<i>Trichomanes bipunctatum</i> Poir.	+	+	-	-	E/r
190	<i>Trichomanes borbonicum</i> Bosch	+	+	+	-	E/r
191	<i>Trichomanes cupressoides</i> Desv.	+	-	+	-	T/r
192	<i>Trichomanes cuspidatum</i> Willd.	-	-	+	-	R
193	<i>Trichomanes digitatum</i> Sw.	-	-	+	-	E/r
194	<i>Trichomanes lenormandii</i> Bosch	+	+	+	-	E
195	<i>Trichomanes longilabiatum</i> Bonap.	+	-	-	-	R
196	<i>Trichomanes mannii</i> Hook.	+	+	+	+	E/r
197	<i>Trichomanes meifolium</i> Bory ex Willd.	-	-	+	-	E
198	<i>Trichomanes melanotrichum</i> Schldtl.	+	+	+	+	E/r
199	<i>Trichomanes montanum</i> Hook. var. <i>montanum</i>	+	+	+	+	E/r
200	<i>Trichomanes montanum</i> Hook. var.? (FR 2907, 2931)	+	+	-	-	R
201	<i>Trichomanes rigidum</i> Sw.	+	+	+	-	T
202	<i>Trichomanes rotundifolium</i> Bonap.	+	+	+	+	E/r
203	<i>Trichomanes speciosum</i> Willd.	+	-	-	-	E/r
204	<i>Vittaria humblotii</i> Hieron.	+	+	+	+	E/r
205	<i>Vittaria isoetifolia</i> Bory ex Fée	-	+	+	+	E
206	<i>Vittaria</i> sp. (FR 3035)	+	+	-	-	E
207	<i>Xiphopteris</i> sp. nov. (FR 3243)	-	-	-	+	E

* Species endemic to Madagascar are indicated in boldface type.

+ = present; - = absent; T = terrestrial; E = epiphyte; R = strictly epilithic; r = occasionally epilithic; L = lianescent. Numerals preceded by the initials FR are the author's collection numbers.

TABLE 3-2. Characteristics of the study plots on the eastern slopes of the RNI d'Andohahela.

	Plot					
	P2	P1	P3	P5	P4	P6
Area (m ²)	800	800	800	800	800	800
Altitude (m)	430	450	820	820	840	1100
Topographic position	middle slope	plateau	middle slope	middle slope	plateau	ravine
Exposure	E		SE	SW	E	W
Slope (°)	20–30	0	15	15–20	2–7	30–45
Canopy height (m)	12–15	20–25	14–16	15–20	16–20	10–16
Woody plant cover (%)	35	35–45	40	35	30–35	20–30
Herbaceous plant cover (%)	7–10	7–12	5–7	15–25	10–35	15–30
Litter thickness (cm)	2	2	5–7	0–2	3	2–4
Humus thickness (cm)	2–5	10–20	15–17	0–10	30	10–30
Soil characteristics	yellow ochre clay	yellow ochre clay–sand	yellow ochre clay	rock (granite)	rock (granite)	brown ochre clay

3. 5–9 individuals or colonies
4. 10–19 individuals or colonies
5. 20–49 individuals or colonies
6. ≥50 individuals or colonies

Note: For small epiphytic species that covered a large, continuous surface on a trunk (species of Hymenophyllaceae and Grammitidaceae), each area of 400 cm² (20 × 20 cm) was arbitrarily considered to represent a single colony. For larger terrestrial or epiphytic gemmiferous species (e.g., *Asplenium sandersonii*² and *A. poolii*), individuals or colonies could be scored easily because all plants connected by a rooted rachis form a colony.

² Authors of the taxa cited in the text are indicated in Table 3-1.

C. The growth form of the species, i.e., whether terrestrial, epilithic, epiphytic, or lianescent. Because many epiphytic pteridophytes can also grow on rocks, as can a more limited number of otherwise terrestrial species, the following growth form categories are recognized:

- T/r, always terrestrial or terrestrial and more rarely epilithic
- E/r, always epiphytic or epiphitic and more rarely epilithic
- R, strictly epilithic
- L, lianescent
- T/E/r, terrestrial, epiphytic, or more rarely epilithic.

Precise definitions of these growth form types

TABLE 3-3. Characteristics of RNI d'Andohahela study plots along watercourses.

	Area (m ²)	Altitude (m)	Width of stream-bed (m)	Nature of streambed	Flow
Plot R1	800 (200 × 4)	420–480	1–3	large granitic rocks + stones	very gentle
Plot R2	800 (200 × 4)	500–530	3–4	large granitic rocks + stones	gentle
Plot R3	800 (200 × 4)	830–840	2–4	large granitic rocks	very gentle
Plot R4	800 (200 × 4)	1450–1460	1–4	large granitic rocks + stones	gentle

TABLE 3-2. *Extended.*

Plot							
P7	P8	P9	P10	P11	P14	P12	P13
800 1150 ridge	800 1280 middle slope	800 1500 lower slope	800 1510 ridge	400 1530 ridge	800 1760 middle slope	800 1830 middle slope	800 1900 middle slope
S	W	E	NE		S-SW	N	W-NW
10-15	35-45	20-30	5	0	5-10	5-10	30-35
12-18	12-16	10-16	12-14	1-12	14-16	8-10	10-14
35-45	35	20-25	40-60	30-40	25-35	20	25-30
5-10	15-30	35-45	3	45-50	7-10	10-15 + moss	5-10
4-8	5-15	7-10	10-15	15	2	0 + moss	5
10-20	20-60	30-50	20-35	10	40	30-60	30-40
brown ochre clay-sand	yellow ochre clay-stony	brown ochre clay-stony	brown ochre clay-sand	yellow ochre clay	yellow ochre clay	stony-sand	yellow ochre clay-sand

are presented elsewhere (Rakotondrainibe & Raharimalala, 1998).

Data Analysis

The data collected from the plots were treated using two classic and complementary types of multivariate analysis (STATITCF, Version 4): correspondence analysis (CA) (Benzécri & Benzécri, 1984; Legendre & Legendre, 1984a,b) and hierarchical ascending classification (HAC) (Jambu, 1978; Legendre & Legendre, 1984b).

The data matrix used for the analyses listed in rows all 162 species recorded in the plot studies against columns representing each of the 18 plots sampled (P1-P14 and R1-R4). Each cell of the matrix contained the corresponding abundance code (1-6) as defined above. For the analyses all of the elements in each column were active.

The two numerical approaches, CA and HAC, provide an estimation of the floristic similarity between plots by comparing the characteristics of each plot in terms of species composition and the importance of each species as a component in each plot. These techniques make it possible to visualize and interpret the structures that occur within the body of the data by χ^2 analysis of the relationships between the different elements (plots

or species) of the matrix. CA yields a representation, in multidimensional space, of the plot and/or species points, and reveals gradients among the data. Correlation between clusters of species and clusters of plots is used to determine characteristic species for each biotope type. HAC generates a tree or dendrogram comprising a hierarchical and progressive grouping of plot and/or species units in sets of increasing size. The criterion used for grouping units into a class is "the average of the weighted distances."

Comparison with the Flora of the RS d'Anjanaharibe-Sud

The pteridophyte flora of the RS d'Anjanaharibe-Sud is compared with that of the RNI d'Andohahela to evaluate the genera and species richness, the number of regional and island-wide endemic pteridophyte species, and the characteristic species in each altitudinal stage. Sørensen's similarity coefficient (Sørensen, 1948) is also used to compare the degree of similarity of the two floras.

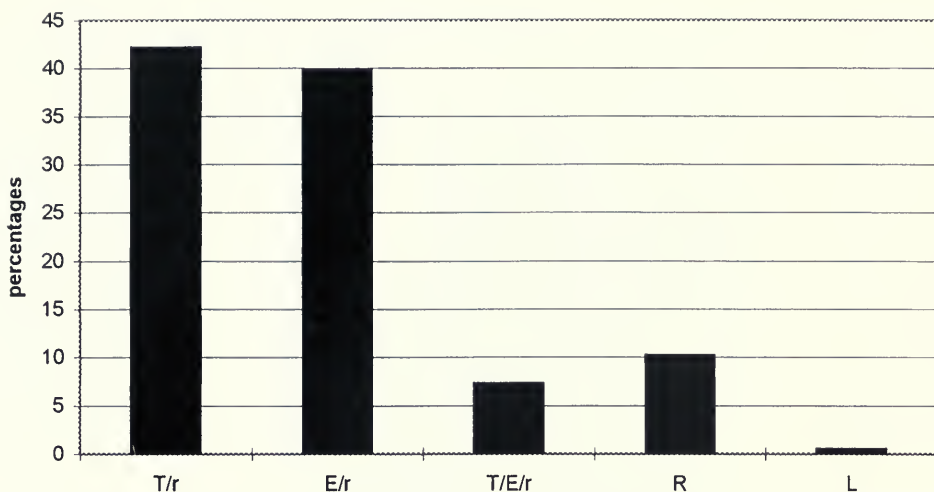


FIG. 3-1. Percentages of the pteridophyte flora (207 species listed in Table 3-1) by habit type in parcel 1 of the RNI d'Andohahela. See Table 3-1 for explanation of abbreviations.

Results

Overall Floristic Analysis

Table 3-1 lists all the taxa observed on the eastern slope of the RNI d'Andohahela between 400 and 1956 m, including those recorded from the 18 plots; their growth form (terrestrial, epiphytic, or epilithic); and their altitudinal distribution. The delimitation of altitudinal zones is explained below.

A total of 207 species or varieties, representing 69 genera, were identified. The most speciose genera were *Asplenium* (27 spp. and three var.), *Elaphoglossum* (20 spp.), *Trichomanes* (14 spp. and one var.), *Cyathea* (12 spp. and two var.), *Huperzia* (nine spp.), *Hymenophyllum* (eight spp.), *Blechnum* (seven spp. and one var.), and *Grammitis* (seven spp.). A large number of genera (52 in all) were represented by only one or two species.

Growth Forms

The histogram of growth form frequencies shown in Figure 3-1 was derived from the data in Table 3-1. A majority of the species and varieties (87, representing 42.2% of the total) were always terrestrial or terrestrial and more rarely epilithic (T/r), 82 taxa (39.8%) were always epiphytic or epiphytic and more rarely epilithic (E/r), whereas only 15 (7.3%) were terrestrial, epiphytic, or more

rarely epilithic (T/E/r). Twenty-one taxa (10.2%) were observed only on rocks (R), and a single species (*Lygodium lanceolatum*) was lianescent (L).

Endemism

Sixty-seven species recorded in parcel 1 are endemic to Madagascar, representing 32.4% of the total pteridophyte flora of the reserve. These taxa are indicated in boldface type in Table 3-1.

Most of the pteridophyte species found on the eastern slope of the RNI d'Andohahela are largely distributed throughout the Eastern and Central domains (*sensu* Humbert, 1955) of Madagascar, although variations occur in their abundance, frequency, and the biotopes they occupy. Some of them (named below) show more restricted distributions, and these are more informative for biogeographical analysis. Our knowledge of the pteridophytes occurring in high mountain areas of Madagascar has progressed substantially in recent years as many new collections have become available, and it is now possible to prepare revised species distribution maps that are probably accurate in most cases.

A description of a new *Xiphopteris* species (Rakotondrainibe 3243), collected as part of the present study, will be published shortly; it is the only taxon that can be considered endemic to the Trafonaomby Massif. This new species was found on two occasions, once as a very inconspicuous

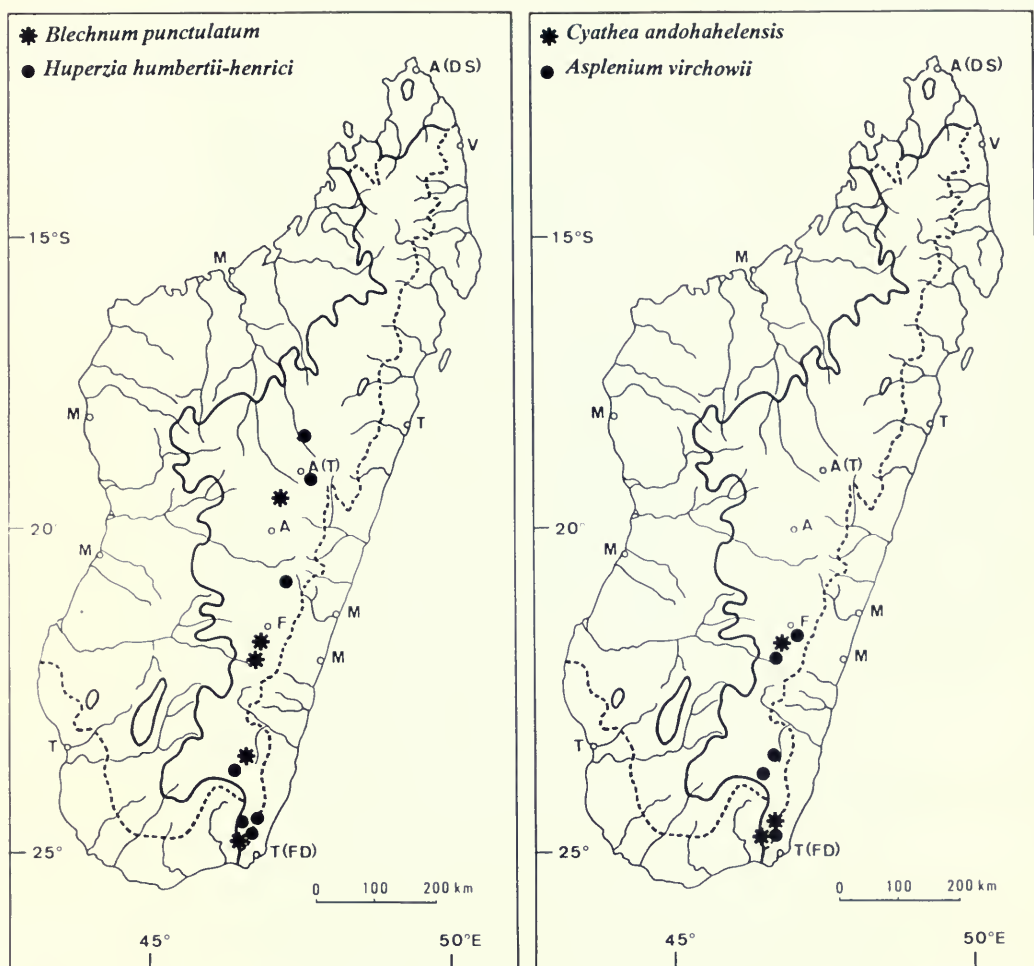


FIG. 3-2. Distribution of several pteridophyte species from parcel I of the RNI d'Andohahela with ranges limited to the South-Central and Mid-Central Domains.

plant occurring at 1300 m and a second time at 1780 m, forming a large epiphytic colony on a single tree trunk in a very wet forest located at the base of a cliff. An *Elaphoglossum* species (Rakotondrainibe 3127) that was found only as a sterile specimen may be new to science and endemic to the massif, but it would be premature to describe it until fertile material can be collected.

Three species endemic to Madagascar are restricted in distribution to the southeastern region of the country: (1) *Cyathea tsilotsilensis* was collected for the first time by Humbert at the Col de Tsilotsilo, 6 km northeast of Elakelaka, and then found again recently on the Andohahela Massif by van der Werff. Along with the material gathered for the present study, the three known collections were made between 400 and 1300 m. (2)

Tectaria madagascariensis was known only from the type collection made by Humbert at 1200 m in a valley between the upper Mananara and the upper Manampanihy. This species can be easily confused with the more widely distributed *T. magnifica*, from which it differs by having a densely hirsute lower surface of the frond and free pinnules of the lower pinnae (Tardieu-Blot, 1958, p. 349). (3) *Ctenitis madagascariensis* has been observed in the mountains south of Tanandava, along a tributary of the Manampanihy, and on Kalambatritra, south of Betroka.

Many species present in the RNI d'Andohahela do not reach much further north than the latitude of Antananarivo (Fig. 3-2) and are characteristic of the Mid-center and South-center subdomains of the Central Domain of Humbert and Cours Darne

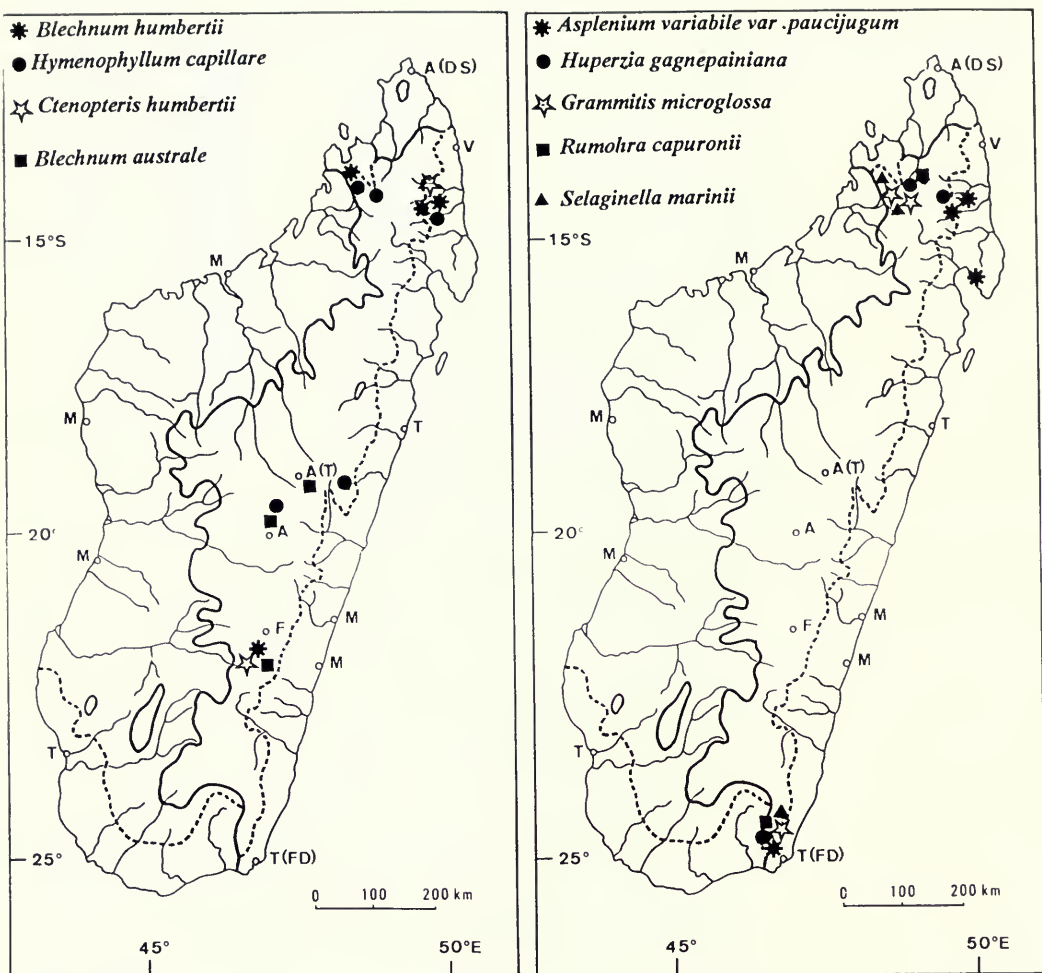


FIG. 3-3. Distribution of several pteridophyte species from parcel 1 of the RNI d'Andohahela with distributions absent from the South-Center Domain (left) and with a disjunct, bipolar pattern (right).

(1965). Examples include *Cyathea andohahelensis* and *Asplenium virchowii*, whose northern distributional limit is the Andringitra Massif. Similarly, *Blechnum punctulatum*, *Huperzia humbertii-henrici*, *Asplenium viviparioides*, *Polystichum coursii*, and *Asplenium lividum* do not reach further north than the RS d'Ambositantely.

The floristic originality of the southwestern region can also be seen in the absence of certain taxa that are more or less widely distributed in other parts of the country. For example, several species, including *Blechnum humbertii*, *Ctenopteris humbertii*, *Hymenophyllum capillare*, and *Blechnum australe* hardly extend south beyond the Tropic of Capricorn (Fig. 3-3, left).

Affinities with Other Mountainous Areas in Madagascar

Several high-altitude species that occur in the RNI d'Andohahela (on the Trafonaomby Massif) are characteristic of the flora present on the highest mountain areas in Madagascar and are common on Tsaratanana, Marojejy, Anjanaharibe-Sud, Ankaratra, and Andringitra. These species include *Ctenopteris flabelliformis*, *Hymenophyllum veronicoides*, and *Huperzia ophioglossoides*, all of which typically occur on ridges; *Lycopodium clavatum*, usually found at forest edges or in the understory of low, open forests at high elevations; *Dryopteris kitchingii*, a heliophilous species that

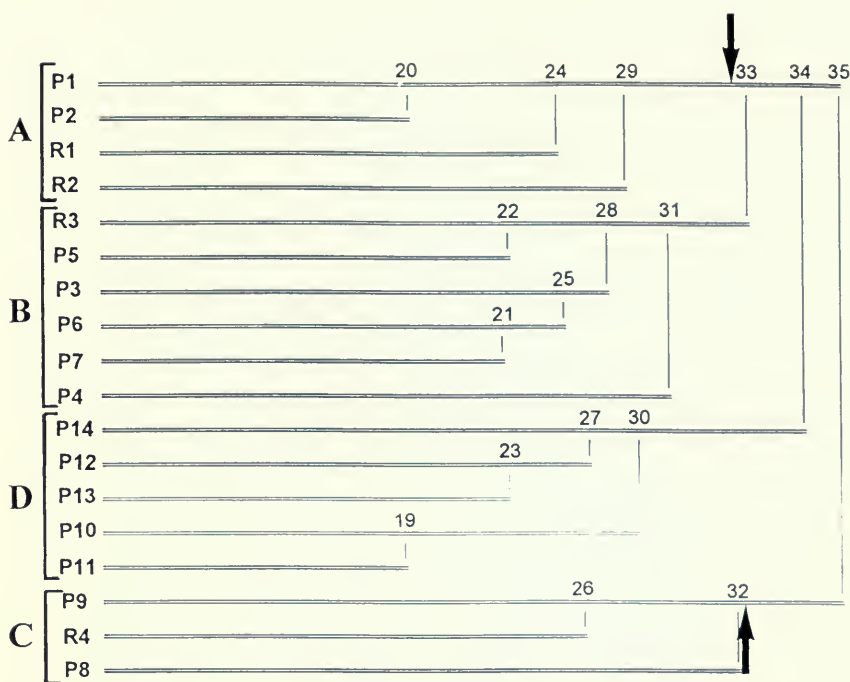


FIG. 3-4. Hierarchical ascending classification (HAC) tree using a matrix of 18 plots (P1–P14, R1–R4) and 162 species of pteridophytes in parcel 1 of the RNI d'Andohahela. The criterion used for grouping units into a class is the average of the weighed distances.

usually grows in rocky crevices; and *Trichomanes meifolium* and *Elaphoglossum aubertii*, both of which occur in more shady areas such as moist depressions surrounded by mosses. *Gleichenia polypodioides*, which is rather common on ridges above 1700–1800 m in several massifs, was collected by Humbert (13505) in 1933 near Pic Trafonaomby but was not seen in 1995.

Finally, current information indicates that seven fern taxa have bipolar north–south disjunct distributions (Fig. 3-3, right). *Asplenium variable* var. *paucijugum* and *Trichomanes montanum* var. ? (Rakotondrainibe 2907) are widespread and common species only at low altitude, between 10 and 600 m in the southern and northern part of Madagascar, but they are absent from the central part, a fact that could be explained by the almost total loss of low-elevation forests on the central part of the island. On the other hand, it is more difficult to explain why species (albeit less common) such as *Blechnum madagascariense*, *Huperzia gagnepainiana*, *Grammitis microglossa*, *Rumohra capuronii*, and *Selaginella marinii*, which generally occur between 810 and 1700 m, are found only in the southern and northern parts of the island, whereas at this elevation range the dense ever-

green forest still covers some areas of the Central Highlands.

Distribution of Taxa

Presence of an Altitudinal Gradient

The tree obtained by HAC from the data matrix of species against study plots is shown in Figure 3-4. By sectioning the tree between nodes 32 and 33, four groups of plots are defined on the basis of the floristic composition of their pteridophytes: group A (comprising P1, P2, R1, and R2), group B (P3–P7 and R3), group C (P8, P9, and R4), and group D (P10–P14). Sectioning the tree at the node immediately below (between nodes 31 and 32) separates P8 from group C.

The positions of groups A through D are shown on axes I–II (Fig. 3-5), I–III (Fig. 3-6), and I–IV (Fig. 3-7). These four axes respectively account for 21.5%, 15.6%, 9.7%, and 8.7% of the inertia of the data points, or 55.5% of the total inertia. For clarity, only structural species are shown, i.e., those contributing to at least 1.8% of the inertia

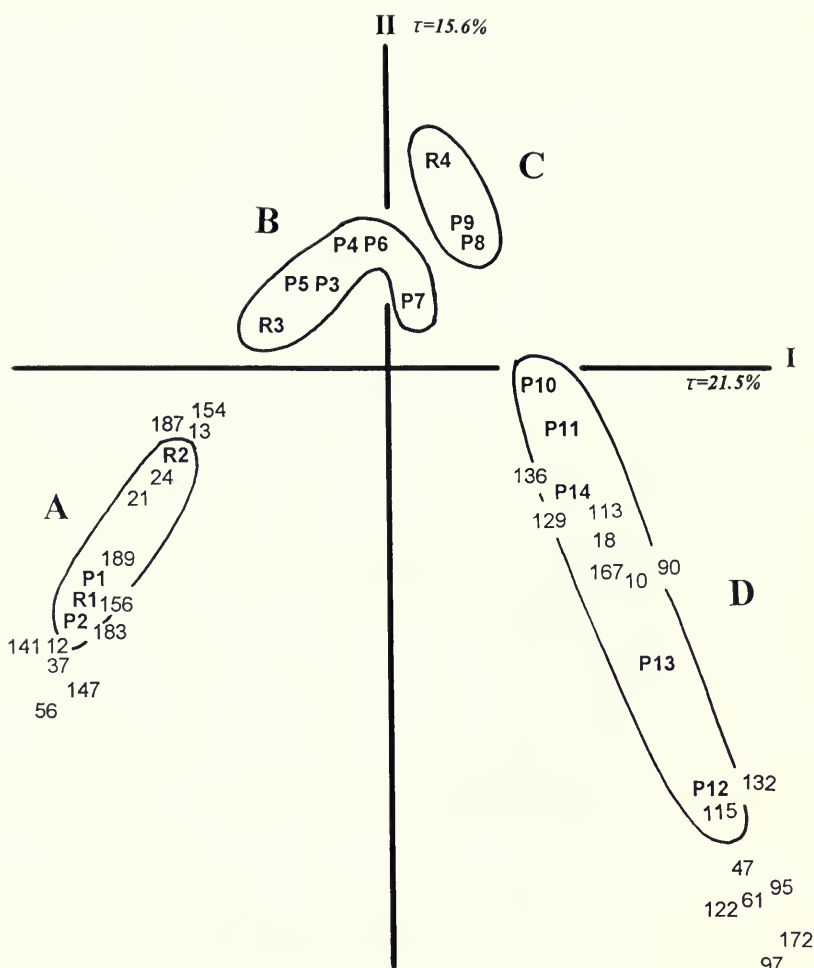


FIG. 3-5. Correspondence analysis (CA) of the matrix of 18 plots and 162 pteridophyte species in parcel I of the RNI d'Andohahela: projection on axes I and II of all of the plots (P1–P14, R1–R4) and the species that contribute to at least 1.8% of the inertia of one or both of the factorial axes. Species numbers are those given in Table 3-1.

of one or both of the factorial axes shown (this cutoff value is explained below). The numerical code for species used in the figures corresponds to those in Table 3-1.

In Figure 3-5, projected on axes I and II, the plots are distributed in a crescent shape (Guttman effect), which indicates the presence of a strong gradient among the data. Axes I and II express the same altitudinal gradient: axis I separates group A, i.e., the plots at low altitude (420–550 m) from group D, i.e., the plots at high altitude (1510–1956 m). Axis II separates groups A and D, located in the negative portion of the scale, from the mid-elevation groups B and C (810–1500 m) in the positive part of the scale.

In Figure 3-6, axis III separates the two mid-

elevation groups, with group B (810–1150 m) in the positive portion and group C (1280–1500 m) in the negative part. Plot P8, which is included in group C (Fig. 3-4), in fact occupies an intermediate position between groups B and C.

In Figure 3-7, the cloud of points comprising group D is stretched along axis IV and is divided into two subunits corresponding to two altitudinal and topographic subgroups. Plots P10 and P11 form one subgroup, located on ridges at 1510–1530 m, whereas P12 and P13, situated on mid-slopes at 1830–1900 m, form a second subgroup. Plot P14, also located on a mid-slope but at 1760 m, is intermediate, which clearly shows that axis IV expresses an altitudinal factor at least in part. The same holds true for the cloud of points mak-

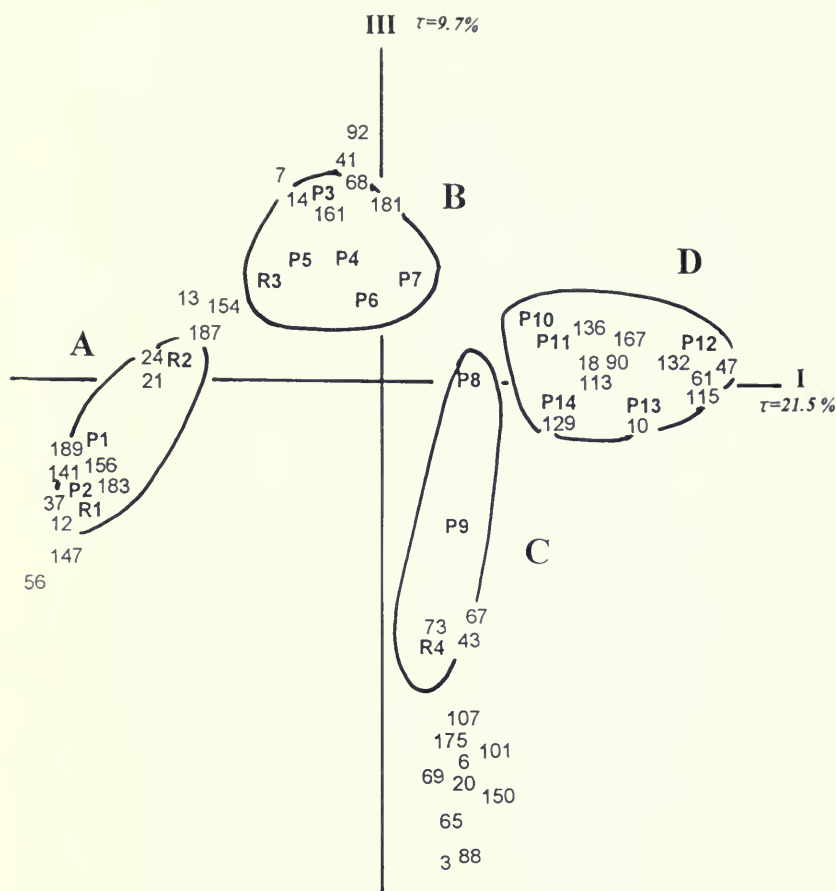


FIG. 3-6. Correspondence analysis of the matrix of 18 plots and 162 pteridophyte species in parcel I of the RNI d'Andohahela: projection on axes I and III of all the plots (P1–P14, R1–R4) and the species that contribute to at least 1.8% of the inertia of one or the other of the factorial axes. Species numbers are those given in Table 3-1.

ing up group C that lie along this axis. Thus, P8, located on a mid-slope at 1280 m, is opposite R4 along a stream at 1450–1460 m, and P9, on a lower slope at 1500 m, is intermediate between them. Groups A and B are compact and contribute only weakly to the expression of factor IV.

The altitudinal gradient, which is also a climatic gradient, thus explains most of the floristic heterogeneity among the plots. Based on the pteridophyte floristic composition, four altitudinal stages can be recognized on the eastern slope of the RNI d'Andohahela: stage A, at low elevations around 420–530 m (P1, P2, R1, and R2); stage B, at lower mid-elevations, between 820 and 1150 m (P3–P7 and R3); stage C, at upper mid-elevations, between 1280 and 1500 m (P8, P9, and R4); and stage D, at high elevations, between 1510 m and the summit at 1956 m (P10–P14).

In the absence of data from between 600 and 700 m, it is not possible to assess the upper limit of stage A. Each of the two lower stages, A and B, is floristically homogeneous (plot points remain clustered on all of the correspondence analysis [CA] projection plans). On the other hand, each of the upper stages is floristically heterogeneous (plot points are stretched along axis II, III, or IV), a fact that reflects both an altitudinal and a topographic gradient, although it is not possible to determine which factor is predominant. Other factors could also influence pteridophyte floristic composition, such as the structure and composition of the soil, the level of human impact in the area, etc., although their influence on the eastern slope of the RNI d'Andohahela appears to be fairly weak and does not alter the general pattern of altitudinal distribution.

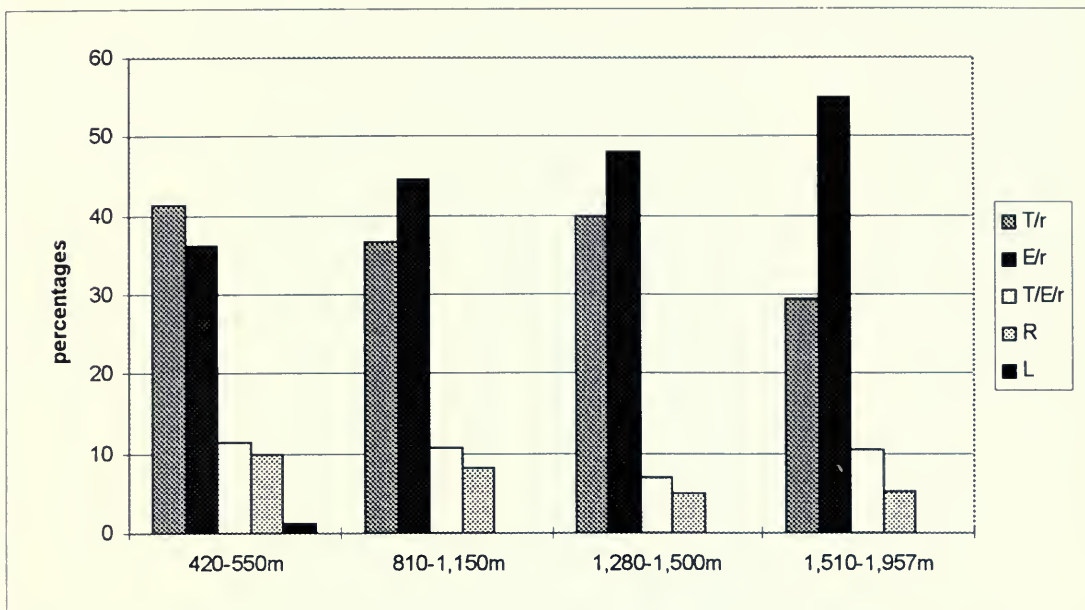


FIG. 3-8. Percentages of pteridophyte flora (207 species listed in Table 3-1) by habit type for each altitudinal zone in parcel 1 of the RNI d'Andohahela. See Table 3-1 for explanation of abbreviations.

two genera are notably speciose, *Trichomanes* (12 spp.) and *Asplenium* (11 spp.). *Cyathea* and *Blechnum* are well represented in the middle altitudinal stages, whereas *Elaphoglossum*, *Huperzia*, and *Grammitis*, all of which are most often epiphytes, are absent or rare at low altitude but become more speciose above 600(?) or 800 m as atmospheric humidity increases due to more frequent fog and mist.

FLORISTIC RICHNESS AT THE SPECIFIC LEVEL—Table 3-5 shows the total number of species recorded at each altitudinal stage, as indicated in Table 3-1, and also the number per unit surface area (100 m²), based on the plot samples.

Overall species richness is highest (123 spp.) between 810 and 1150 m, where the habitat is very diversified. Higher in elevation, between 1280 and 1500 m, forest structure is simpler, more uniform, and the number of species present (100 spp.) is lower despite their being more numerous per unit area (6.7 per 100 m² vs. 5.5 per 100 m² at lower elevations).

ALTITUDINAL INDICATORS—In an attempt to assess the ecological status of each species, information from the general inventory (Table 3-1) was used along with the results from the statistical analyses of the plot samples. The first three axes of the CA of the plot-species matrix are interpreted as altitudinal factors, whereas the fourth

axis appears to be either an altitudinal or a topographic factor, or possibly both. Consequently, only species that contribute substantially to the inertia of at least one of the three first axes (contribution [CTR] $\geq 1.8\%$) are regarded as useful altitudinal indicators. A total of 48 species meet these criteria (Table 3-7). The value of 1.8% was chosen *a posteriori* as the threshold because it eliminates species that are too widely distributed, those that are infrequent, and those with an erratic distribution.

Indicator species that are restricted to a single altitudinal stage are referred to as “exclusively characteristic” of that stage (see Table 3-7). Those that are significantly more abundant statistically in a given stage than elsewhere (i.e., those that have higher coefficients of abundance in the constituent plots) and have a CTR $\geq 1.8\%$ are called “preferentially characteristic” (see Table 3-7). Exclusively characteristic species are shown in boldface type and preferentially characteristic species are shown in normal type in Table 3-7. Group 1 species are characteristic of the low-elevation stage A; those in group 2 are characteristic of stage B at mid-elevations; group 3 is characteristic of mid-elevation stage C; and group 4 is characteristic of stage D at high altitudes. The species in groups 5 and 6 are characteristic, respectively, of stages A + B and C + D.

TABLE 3-4. Pteridophyte habit type for each altitudinal zone.

	420–550 m	810–1150 m	1280–1500 m	1510–1957 m
T/r	41.3%	36.6%	40.0%	29.5%
E/r	36.2%	44.7%	48.0%	55.1%
T/E/r	11.3%	10.6%	7.0%	10.3%
R	10.0%	8.1%	5.0%	5.1%
L	1.2%	0 %	0 %	0 %

See Table 3-1 for explanation of abbreviations.

Conclusions and Discussion

The pteridophyte flora of the eastern slope of the RNI d'Andohahela comprises 207 species and varieties that represent 69 genera. One of them, an undescribed species of *Xiphopteris* (Rakoton-drainibe 3243), is currently the only known taxon endemic to the massif, whereas three other taxa are endemic to the southeastern region of Madagascar.

The results of the quantitative floristic analysis make it possible to recognize four altitudinal stages within the study area:

Stage A, at low elevations between 420 and 550 m, occupied by dense, moist evergreen forest. A total of 40 genera and 80 species or varieties of ferns, five of which are exclusively characteristic species, were found in this formation. The genera *Trichomanes* (12 spp.) and *Asplenium* (11 spp.) are dominant in terms of the number of spe-

cies present. The average density of pteridophyte species is 3.7 per 100 m². Terrestrial species are most numerous (41.3%), whereas epiphytes represent 36.2% of the total, and epiliths 10.0%.

Stage B, at lower mid-elevations between 810 and 1150 m, with dense, moist montane forest in which 49 genera and 123 species or varieties of ferns were recorded. *Asplenium* is clearly dominant (24 spp.); *Elaphoglossum* (10 spp.) and *Cyathea* (9 spp.) are well diversified. No species is restricted to this stage, and the average species density is 5.5 per 100 m². Epiphytic species are dominant (44.7%), indicating an increase in relative atmospheric humidity as compared to stage A, at low elevation. Terrestrial species are nevertheless well represented (36.6%), and strictly epilithic species are more rare (8.1%).

Stage C, at upper mid-elevations between 1280 and 1500 m, which is in fact a transition between dense, moist montane forest and the sclerophyl-

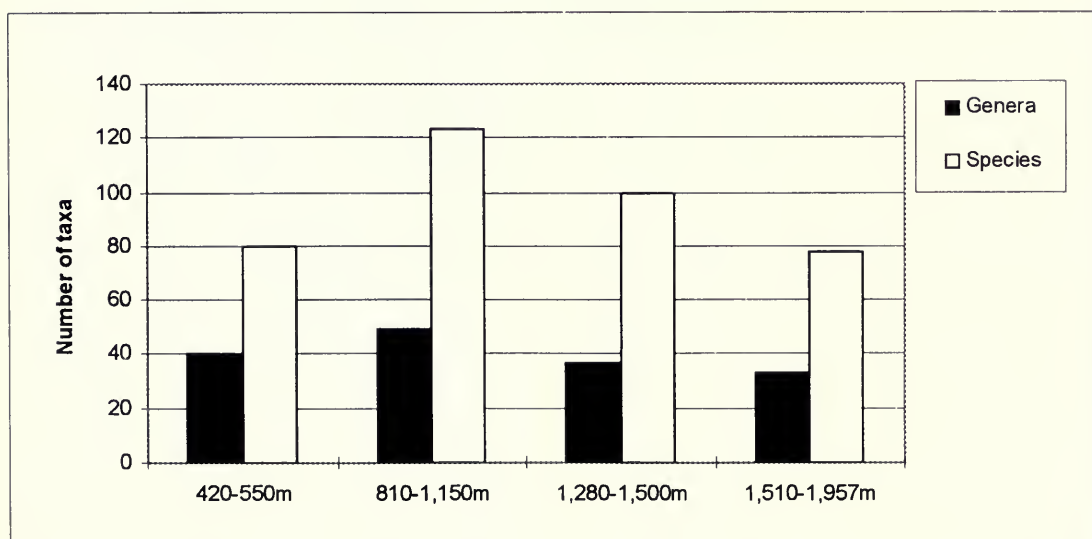


FIG. 3-9. Generic and specific floristic richness of pteridophytes (207 species listed in Table 3-1), at each altitudinal zone, in parcel 1 of the RNI d'Andohahela.

TABLE 3-5. Generic and specific richness for each altitudinal zone.

	420–550 m	810–1150 m	1280–1500 m	1510–1957 m
Genera (total number)	40	49	37	33
Species (total number)	80	123	100	78
Number of species/100 m ²	3.7	5.5	6.7	3.5

lous forests of the highest stage. An intermingling of the forest types characteristic of the stages above and below results in a particularly high average species density (6.5 spp. per 100 m²), balanced percentages of epiphytic and terrestrial species (48.0% and 40.0%, respectively), and a certain level of heterogeneity in the flora that can be seen along a topographic and altitudinal gradient. One hundred species, eight of which are exclusively characteristic, were recorded in this stage. The dominant genera are *Asplenium* (13 spp.), *Trichomanes* (11 spp.), and *Elaphoglossum* (10 spp.).

Stage D, at high elevations between 1510 and 1956 m, occupied by montane sclerophyllous forest that includes 33 genera and 78 species of ferns, of which seven are exclusively characteristic. Epiphytic species are highly dominant (55.1%) as compared to terrestrials (29.5%). The most diversified genera are *Asplenium* (13 spp.) and *Elaphoglossum* (10 spp.).

A comparison of the the pteridophyte flora of the RNI d'Andohahela with that of the RS d'Anjanaharibe-Sud, located in the northern part of the island (Rakotondrainibe & Raharimalala, 1998), makes it possible to develop a better understanding of the factors responsible for its current composition. Comparative data are presented in Table 3-8. Note that the studies conducted in these two reserves were essentially identical: fieldwork covered a 2-month period at the same time of year in each case and was conducted using identical methods.

(1) Despite its position in extreme southern Madagascar, outside of the Tropic of Capricorn, the RNI d'Andohahela has a pteridophyte flora as rich as that of the RS d'Anjanaharibe-Sud, where 211 species and varieties were recorded in 1994 (Rakotondrainibe & Raharimalala, 1998). A large portion of the flora is shared between the two areas (121 species and varieties, representing 50% of the taxa in each of the reserves), giving a Sørensen's similarity coefficient of 57.9 ($200 \times 121/207 + 211$). The two reserves have many other aspects in common. They are both situated on ancient granitic massifs that reach approximately the same elevation (1956 m and 2064 m, respectively), and they fall within the same bioclimatic stages: the humid stage at low altitudes, the sub-humid stage above about 600–800 m, and the montane stage above ca. 1800 m (Cornet, 1974). These stages are characterized by high rainfall and/or extended periods of mist and fog.

(2) At the same time, the fact that the two reserves are located some 1450 km apart and at opposite ends of Madagascar (one in the far south and the other in the extreme north), separated by about 10° of latitude, results in substantial climatic differences between them (Table 3-9). The coastal towns Tolagnaro in the south and Antalaha in the north were chosen for comparing the climates of the two regions in which the reserves are located, primarily because of their proximity to the study zones and the availability of complete meteorological records covering many years. Although Tolagnaro is in the same bioclimatic stage as An-

TABLE 3-6. Species richness of the eight largest pteridophyte genera for each altitudinal zone.

Genus	420–550 m	810–1150 m	1280–1500 m	1510–1957 m	Total: 420–1957 m
<i>Asplenium</i>	11	24	13	13	30
<i>Elaphoglossum</i>	4	10	10	10	20
<i>Trichomanes</i>	12	9	11	4	15
<i>Cyathea</i>	4	9	8	2	14
<i>Huperzia</i>	0	6	6	6	9
<i>Hymenophyllum</i>	3	5	6	6	8
<i>Blechnum</i>	1	3	6	2	8
<i>Grammitis</i>	0	1	4	4	7

TABLE 3-7. Coefficients of abundance for indicator species of altitude in the 18 study plots (P1–P14 and R1–R4).

Taxa	Altitude (m):																	
	420–550 Stage A						810–1150 Stage B						1280–1500 Stage C					
	P1	P2	R1	R2	P3	P4	P5	R3	P6	P7	P8	P9	R4	P10	P11	P12	P13	P14
Group 1																		
<i>Asplenium bipartitum</i>	5	6	5	5														
<i>Asplenium variabile</i> var. <i>paucijugum</i>	6	6		3														
<i>Ctenitis cirrhosa</i>	1	5	5															
<i>Lygodium lanceolatum</i>		6	4	2														
<i>Selaginella pectinata</i>	2	4	4	5														
<i>Asplenium nidus</i>	6	6	6	5	4	4	4	4		1								
<i>Lomariopsis</i> aff. <i>pollicina</i> (FR 2860)	6	6	4	5														
<i>Nephrolepis biserrata</i>	4	4	5	5	2													
<i>Trichomanes bipunctatum</i>	5	6	1	6		2												
Group 2																		
<i>Antrophyum malgassicum</i>				3	3	6	3	3										
<i>Asplenium cuneatum</i>			1	5	6	5	6	4	5	4								
<i>Belvisia spicata</i>					3	2	3		3	3								
<i>Cyathea borbonica</i> var. <i>laevigata</i>					1	5	3	1	6	3								
<i>Elaphoglossum</i> aff. <i>sieberi</i> (FR 2962)					4	6	1		2									
<i>Pellaea angulosa</i>				2	4		6	3	1	4	3							
Group 3																		
<i>Antrophyum boryanum</i>													4				3	
<i>Asplenium herpetopteris</i> var. <i>massoulae</i>													5				6	
<i>Blechnum attenuatum</i> var. <i>giganteum</i>											6		6				6	
<i>Cyathea</i> aff. <i>dregei</i> (FR 3122)													1				4	
<i>Cyathea</i> aff. <i>bellisquamata</i>											5		4				5	
<i>Cyathea borbonica</i> var. 1 (FR 3150)												2	3					
<i>Dryopteris manniana</i>													5					
<i>Pteris griseoviridis</i>											1	6	6				5	
<i>Anauropelta bergiana</i>													5				5	
<i>Cyathea decrescens</i>					3								5				6	
<i>Elaphoglossum humbertii</i>													5				4	
<i>Elaphoglossum</i> sp. 9 (FR 3127)													5				3	
<i>Megalastrum lanuginosum</i>													5				6	

TABLE 3-7. Continued.

Taxa	Altitude (m):			420–550 Stage A			810–1150 Stage B			1280–1500 Stage C			1510–1957 Stage D					
	P1	P2	R1	R2	P3	P4	P5	R3	P6	P7	P8	P9	R4	P10	P11	P12	P13	P14
Group 4																		
<i>Blechnum punctulatum</i>																6	6	
<i>Ctenopteris flabelliformis</i>																6	4	
<i>Elaphoglossum angulatum</i>																5	4	
<i>Elaphoglossum coursii</i>																6		
<i>Grammitis</i> sp. nov. 1 (FR 3197, 3230)																5	6	2
<i>Hymenophyllum veronicoides</i> C. Chr.																6	4	4
<i>Pteridium aquilinum</i>																4		
<i>Elaphoglossum acrostichoides</i>											4	2		3	6	6	5	
<i>Huperzia ophioglossoides</i>																4	3	
<i>Pleopeltis macrocarpa</i>						2			1	3				3	5	6	6	5
Group 5																		
<i>Asplenium blastophorum</i>	6	5		5	4	3	4	5		2								
<i>Asplenium inaequilaterale</i>	6	6	6	6			6	6	3									
<i>Microsorium punctatum</i>	4	4	4	6	3	5	6	5	2	3								
<i>Tectaria madagascariensis</i>	3	1	6	6			5	6	6									
<i>Schizaea dichotoma</i>					6	6				6	6							
Group 6																		
<i>Grammitis holophlebia</i>											5	4		2	6	6		5
<i>Asplenium aethiopicum</i>												2	2	3	3	5	5	4
<i>Hymenophyllum polyanthos</i>						5					3	5	2		5	6	5	3
<i>Asplenium friesiorum</i>						2				2	2	4		3	3	6	5	4
<i>Lepisorus excavatus</i>						1			2	3	4	2		3	5	5	5	3

Note: exclusively characteristic species are indicated in boldface type. Preferentially characteristic species are in normal type face. See text for definitions of characteristic species and values of abundance classes.

TABLE 3-8. Species richness, endemism, and degree of similarity of the pteridophyta flora of the RNI d'Andohahela and RS d'Anjanaharibe-Sud.

Parameter evaluated	RNI d' Andohahela	RS d' Anjanaharibe-Sud	Ps
Total number of species and varieties	207	211	57.9
Total number of endemic Malagasy species	67 (32.4%)	82 (38.9%)	
Total number of species endemic to the massif	1	5	
Number of species between 400 and 600 m	80	52	45.5
Number of species between 800 and 1100 m	123	113	46.6
Number of species between 1250 and 1500 m	100	122	49.5
Number of species between 1550 and 2000 m	78	117	32.8

Ps = Sørensen's coefficient of similarity.

talaha, its climate is markedly drier and cooler. Average annual precipitation differs by 613 mm, and the average number of days with rainfall is greater by 60.4 days at Antalaha. Average relative humidity is similar (differing only by 5%), but both stations are located close to the sea, and in light of the difference in rainfall it is likely that humidity levels are more divergent farther inland. The only substantial differences in average temperatures between the two stations are those of the minima; the average temperature during the coldest month is 2.8°C higher at Antalaha, but that for the warmest month differs by only 0.3°C. The difference in average temperatures between the warmest and coldest months is 14.2°C at Tolagnaro and 11.7°C at Antalaha. The recorded differences in rainfall and temperatures between the two regions, associated with varying degrees of human impact, can thus explain (at least in part) the observed differences in the overall floristic composition and in the altitudinal distribution of floristic richness in the two reserves (Table 3-8).

The genera *Hymenophyllum* and *Ctenopteris*, most of whose species are epiphytes that prefer moist microhabitats, are abundant in the high-elevation formations; they are less speciose in the

RNI d'Andohahela (with 8 and 5 spp., respectively) than in the RS d'Anjanaharibe-Sud (14 and 9 spp.). By contrast, *Asplenium*, the species of which are much more tolerant of short dry periods, is more diverse in the RNI d'Andohahela (30 vs. 26 spp. in the RS d'Anjanaharibe-Sud), especially between 810 and 1100 m (24 vs. 17 spp.).

Between 400 and 1100 m overall pteridophyte species richness is higher in the RNI d'Andohahela, a trend that is reversed starting at 1280 m. This can be interpreted as follows: on the eastern slope of the RS d'Anjanaharibe-Sud the low-elevation moist evergreen forest is now largely destroyed and covers only a small area. On the other hand, this formation is still extensive and well preserved in the RNI d'Andohahela, although clear signs of earlier human presence, such as funerary monuments, are evident (see Chapter 1). Above 1250 m the presence of more pteridophyte species in the RS d'Anjanaharibe-Sud is most likely the consequence of a climate more favorable to their growth (smaller difference in average temperature and higher average annual precipitation) and almost certainly is also due to the proximity of another large mountain massif, Marojejy. Marojejy must play a role as a local source of diaspores,

TABLE 3-9. Average meteorological data from Tolagnaro and Antalaha.

Stations	Annual precipitation (mm)	Number of days with rainfall	Relative humidity (%)	Temperature during the warmest month (M)	Temperature during the coldest month (m)	M - m
Tolagnaro	1537.1	152.8	76	29.5	15.3	14.2
Antalaha	2150.3	213.2	81	29.8	18.1	11.7

Rainfall and temperature data are from Morat (1969); relative humidity data are from Chaperon et al. (1993). Morat (1969) used data from 1931–1960 for both cities; Chaperon et al. (1993) did not indicate the source of their data, but they were taken prior to 1970 (Chaperon, pers. comm.).

thereby increasing the total area of high-altitude habitats within the region.

(3) The floristic similarities observed between the two study areas, as expressed by the Sørensen's coefficient (Ps), are comparatively strong between 400 and 1500 m ($45.5 \leq Ps \leq 49.5$), but are much weaker starting at 1500 m ($Ps = 32.8$). However, this coefficient only takes into consideration the presence or absence of species. If abundance values are used, a somewhat different interpretation results; the floristic similarities become evident between 400 and 1150 m, and the two massifs share eight exclusively or preferentially characteristic species within this altitudinal range (*Asplenium bipartitum*, *A. cuneatum*, *A. inaequilaterale*, *A. nidus*, *A. variabile* var. *paucijugum*, *Lygodium lanceolatum*, *Microsorium punctatum*, and *Nephrolepis biserrata*). Above 1280 m only one shared species (*Asplenium friesiorum*) is an altitudinal indicator, and with the exception of this taxon, the upper portions of the two massifs have completely different characteristic species, reflecting much weaker levels of floristic similarity. These results demonstrate the importance of comparative studies of pteridophytes that take into consideration not only the presence (or absence) of the species but also their abundance.

(4) The data currently available indicate that the level of specific endemism is lower in the RNI d'Andohahela than in the RS d'Anjanaharibe-Sud. A total of 32.4% of the fern taxa recorded in the RNI d'Andohahela are endemic to Madagascar and one species is restricted to the Trafonaomby Massif, whereas 38.9% of the taxa at RS d'Anjanaharibe-Sud are Madagascar endemics and five are known only from the Anjanaharibe-Sud Massif. However, botanical exploration is far from complete in southeastern Madagascar, especially with respect to pteridophytes, for which the specimen base in national and international botanical institutions remains small.

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Appendix 3-1

The Pteridophytes of Parcel 2 of the RNI d'Andohahela

An inventory of the pteridophytes of parcel 2 of the RNI d'Andohahela was conducted at low elevation (150–180 m) along the Mananara River, 7.5 km NNE of the village of Hazofotsy. The region is situated within the subarid bioclimatological stage (Cornet, 1974), characterized by an average annual minimum temperature between 10° and 13°C, a cumulative water deficit of 300–400 mm, and a dry season of 9 months. The vegetation present on sandy-clay soils is a low open xeric forest that is rich in *Commiphora*, *Diospyros*, *Euphorbia*, *Pachypodium*, and *Alluaudia*. Sandy and calcareous soils and rocky outcrops are covered by a xeric thicket that is dominated by Didiereaceae and Euphorbiaceae. Fieldwork was conducted during a 3-day period within a 2 km radius around our base camp. A phytoecological study was done in low xeric forest within a 200 m² plot (P15) established on a gentle slope (15°) with eastern exposure. The distribution of pteridophytes in this dry formation was highly heterogeneous, with the species density per 100 m² ranging between 0 and 4. The location of the plot was chosen so that as many species as possible would be included (i.e., eight species in the 200 m² samples).

The 11 species of ferns recorded in the dry formations within parcel 2 are listed in Table A3-1. Five of them (in boldface type), including three species of *Selaginella*, are endemic to Madagascar. None of the species occurs in the Eastern Domain. *Adiantum capillus-veneris* and *Doryopteris madagascariensis* are widely distributed in Madagascar, including in the Sambirano, Central, Western, and Southern domains. All of the other species are limited to the Western and Southern domains.

TABLE A3-1. Pteridophytes of parcel 2 of the RNI d'Andohahela.

Taxa*	Frequency	Habit type	Ecology
<i>Actiniopteris radiata</i> (Koenig ex Sw.) Link	++	terrestrial	rocky soil
<i>Adiantum capillus-veneris</i> L.	+	terrestrial	stream bank
<i>Doryopteris concolor</i> (Langsd. & Fisch.) Kuhn	+	terrestrial	open understory
<i>Doryopteris madagascariensis</i> Tardieu	++	terrestrial	open understory
<i>Doryopteris pilosa</i> (Poir.) Kuhn	+	terrestrial	open understory
<i>Notholaena lanceolata</i> Bonap.	++	terrestrial	rocky soil
<i>Pallaea calomelanos</i> (Sw.) Link.	+	terrestrial	clay slope
<i>Pallaea viridis</i> (Forssk.) Prantl var. <i>glauca</i> Sim.	+	terrestrial	open understory
<i>Selaginella digitata</i> Spring	+++	terrestrial	open understory
<i>Selaginella helicoclada</i> Alston ex Alston	+	terrestrial	open understory
<i>Selaginella proxima</i> R. M. Tryon	+++	terrestrial	open understory

* Species endemic to Madagascar are indicated in boldface type.

+ = rare (seen 1 to 5 times); ++ = infrequent (seen 6 to 20 times); +++ = frequent (seen 21 to 50 times).

Chapter 4

Structure and Floristic Composition of the Vegetation in the Réserve Naturelle Intégrale d'Andohahela, Madagascar

Pierre Jules Rakotomalaza¹ and Nathalie Messmer²

Abstract

Studies were undertaken on the vegetational structure and floristic composition of five 1 ha plots in the humid forest of parcel 1 of the Réserve Naturelle Intégrale (RNI) d'Andohahela. These five plots were established along an altitudinal gradient between 440 and 1875 m. A total of 4,875 trees (≥ 10 cm dbh) covering 359 species and 48 plant families were recorded. The number of species per hectare ranged from 52 to 147. The total number of trees per hectare varied between 675 and 1,365 individuals. Total basal area varied from 34.1 to 65.9 m². No one plant dominated all of the five study plots. Few species dominated each plot; 50% of the trees with dbh ≥ 10 cm were represented by between nine and 18 species. Thus, the Shannon-Weaver diversity index showed very low values. Data from these plots were first analyzed individually and then compared between plots in order to document floristic and structural variation along the elevational gradient. The patterns found in parcel 1 of the RNI d'Andohahela are compared to other sites in Madagascar, as well as to other areas in Asia, Africa, and South America.

Studies were also conducted in the spiny forest of parcel 2 of the RNI d'Andohahela. Ten linear transects ("Gentry transects"), with a total surface area of 0.1 hectare, were established. Trees with a dbh ≥ 2.5 cm were censused. Of the 607 individuals, 540 plants were identified as belonging to 85 species in 28 families. The Shannon-Weaver diversity index value for this site was very low due to the dominance of a few families and species. These results are compared with another spiny forest in southern Madagascar and with sites in the Neotropics and Africa.

Résumé

Un inventaire floristique quantitatif et qualitatif de la forêt dense humide de la Réserve Naturelle Intégrale (RNI) d'Andohahela (parcelle 1) d'une part, ainsi que de la forêt dense sèche de la RNI d'Andohahela (parcelle 2) d'autre part, a été effectué. Dans la forêt dense humide de la parcelle 1 de la RNI d'Andohahela, cinq parcelles permanentes d'un hectare chacune ont été mises en place en un gradient altitudinal s'échelonnant de 440 m à 1875 m d'altitude. Un total de 4,875 arbres de diamètre à hauteur de poitrine (dbh) égal ou supérieur à 10 cm, comptant 359 espèces and 48 familles de plantes a été recensé. Le nombre d'espèces par hectare s'étend de 52 à 147. Le nombre total d'arbres par hectare varie entre 675 et 1,365 individus. L'aire basale total varie entre 34.1 et 65.9 m². Aucune plante ne domine dans les cinq parcelles permanentes. Et même si le nombre d'espèces dans chaque plot n'est en rien

¹ Missouri Botanical Garden, B.P. 3391, Antananarivo (101), Madagascar.

² Conservatoire et Jardin Botaniques de la Ville de Genève, Case Postale 60, CH-1292 Chambésy/Genève, Switzerland.

extrême, le nombre d'espèces dominant chaque parcelle permanente est faible, à savoir entre neuf et dix-huit espèces représentent les 50% des arbres de dbh ≥ 10 cm. En conséquence, les valeurs de l'indice de diversité de Shannon-Weaver sont très basses. Ces parcelles permanentes d'un hectare ont d'abord été analysées individuellement et ensuite mises en relation les unes par rapport aux autres, afin de mettre en évidence les variations floristiques et structurales en fonction de l'altitude. Ces résultats sont comparés à ceux d'autres sites à Madagascar, ainsi qu'en Asie, Afrique et Amérique du Sud.

Un inventaire floristique effectué dans la forêt dense sèche de la parcelle 2 de la RNI d'Andohahela a également été mené. Dix transects linéaires de Gentry, totalisant une surface de 0.1 hectare, ont été mis en place. 607 individus de dbh ≥ 2.5 cm ont été recensés, dont 540 ont été déterminés, appartenant à 85 espèces et 28 familles. La valeur de l'indice de diversité de Shannon-Weaver est très basse, à cause de la dominance de quelques espèces et familles. Ces résultats ont été comparés à un autre site du sud de Madagascar, ainsi que des sites dans les Néotropiques et en Afrique.

Introduction

The Réserve Naturelle Intégrale (RNI) d'Andohahela, with its three noncontiguous parcels, contains a remarkable range of vegetation types. These parcels consist of parcel 1, a large zone of humid forest along the eastern slope of the Anosyenne Mountains that contains lowland forest to high mountain forest; parcel 2, with spiny forest and gallery forest; and parcel 3, with a form of transitional habitat between humid and spiny forests (see Chapters 1 and 2). During the 1995 inventory of parcels 1 and 2 our intent was not simply to conduct a qualitative survey of the local plant species, but also to make a quantitative assessment of floral and structural aspects of these forests.

Given the differences in vegetation between parcels 1 and 2, combined with time limitations inherent to rapid surveys, we were faced with methodological constraints and had to use two different survey techniques, which are discussed in detail below. Accordingly, this report is divided into two parts. The first part addresses vegetation in the humid forest of parcel 1. Humid forests are usually divided into vegetation zones associated with elevational bands that are based on quantitative characteristics (e.g., diameter at breast height [dbh], height, canopy width) and floristic attributes. The second part of this chapter concerns the spiny forest of parcel 2. Few studies of forest composition and structure have been conducted on this vegetational type. Our specific objectives for both forest types were (1) to provide a quantitative account of the study sites; (2) to provide a comparison of floristic composition between plots established at different elevations in

the humid forest (parcel 1); (3) to document the vegetational changes along the elevation gradient in the humid forest (parcel 1); and (4) to augment available information on the flora and structure of the spiny forest (parcel 2).

A qualitative and quantitative survey requires sampling. Plots are quantitative, potentially rigorous statistically, and provide a good measure of the structure, floristic composition, and vegetation variability. Transect sampling is a rapid method that uses less sophisticated measurements. These qualitative (identification by scientific name) and quantitative (number, dbh, and height) data provide a basis with which to assess physical parameters (e.g., distribution of dbh and height) between different elevations or formations, density, dominance, frequency, and species diversity. On the basis of this information it is possible to quantify diversity at each site. General collections were made in each altitudinal zone that allow species lists for each site to be further supplemented; identifications were generally limited to fertile individuals.

Ecologists have devoted considerable effort to developing various indices of diversity that factor in aspects of both the number of species and their relative densities. One of the most frequently used is the Shannon-Weaver diversity index (Shannon & Weaver, 1949). Each plot was analyzed separately and then compared to the others using the Shannon-Weaver diversity index and the Horn similarity index (Goldsmith et al., 1986).

Methods

The quandary that has hindered developments in the quantification of tropical plant communities

during rapid assessments is that the sampling area needs to be big enough to contain a sufficiently large number of species that are representative of the local community, yet small enough to be practicably and rapidly studied. Botanists often make numerous counts or collect specimens of redundant common and easily accessible species and overlook rarer and less obvious species. For the RNI d'Andohahela inventory, sampling and data collections were conducted in five 1 ha permanent plots established at five different altitudinal zones in parcel 1 and in ten transects ("Gentry transects") in parcel 2.

Sampling Procedure and Study Sites

PERMANENT PLOTS—One-hectare permanent plots have been established in other forests of Madagascar largely on the recommendation of the Missouri Botanical Garden. Three 1 ha permanent plots were installed and sampled in the humid forest of Parc National (PN) de Ranomafana (Schatz, 1994); two on the Masoala Peninsula; one in the RS d'Ambositantely (Rabevohitra et al., 1996; C. Birkinshaw, pers. comm.); and ten along the east coast: Tampolo (Fenerive est), Andranomintina (Masoala), Tanambao (Manajary), Réserve Spéciale (RS) de Manombo (Farafangana), and Ste. Luce (Tolagnaro).

Permanent plots provide both quantitative and floristic data that, with continued sampling, permit analyses of growth rates and forest dynamics. Diameter at breast height was measured 1.44 m off the ground (Malcomer, 1991) and not at the more standard height of 1.3 m off the ground (CFT, 1989). Trees of ≥ 10 cm dbh were marked with numbered metal tags, their dbh measured, and their height estimated from ground level. Voucher specimens, even sterile, were collected. Material from fertile plants was later compared with material housed in the herbaria of the Parc Botanique et Zoologique de Tsimbazaza (PBZT) and the Direction des Ressources Forestières et Piscicoles (DRFP), Antananarivo. The nonfertile material was assigned to a "morphospecies" when a binomial name could not be determined (Malcomer, 1991), and these morphospecies are numbered sequentially.

With the exception of the plot at 1875 m, all of the sites were located close to our camps in parcel 1. Owing to difficulties in capturing satellite signals with a global positioning system in forest with a thick canopy, the coordinates of the

1 ha plots given below are those for the adjacent camp sites (Chapter 1, Fig. 1-1). The coordinates for the 1875 m site come from the nearby forest edge.

The following plots were established:

- Plot 1—440 m, established near the Andranohela River, 8.0 km NW of the village of Eminiminy, 24°37.6'S, 46°45.9'E. Shape 500 × 20 m.
- Plot 2—840 m, placed near a tributary of the Andranohela River, 12.5 km NW of the village of Eminiminy, 24°35.6'S, 46°44.3'E. Shape 200 × 50 m.
- Plot 3—1150 m, on a plateau 13.5 km NW of the village of Eminiminy, 24°35.0'S, 46°44.1'E. Shape 100 × 100 m.
- Plot 4—1550 m, 15.0 km NW of the village of Eminiminy, 24°34.2'S, 46°43.9'E. Shape 250 × 40 m.
- Plot 5—1875 m, established on the plateau just below Pic Trafonaomby (1959 m), 20 km SE of the village of Andranondambo, 24°33.7'S, 46°43.3'E. Shape 200 × 50 m.

In each elevational zone general plant collecting was conducted outside the plots for additional floristic information.

LINEAR TRANSECTS—The linear transect method has proved to be satisfactory for analyses of structural and floristic composition (Gentry, 1982). For example, using this method Gentry (1988) sampled 130 different forests at about 70 sites in four high-species-diversity areas of the world. In Madagascar, this approach has been used previously in dry deciduous forests (Gentry, 1988; Du Puy et al., 1994).

Our quantitative and qualitative floristic inventory was conducted in the spiny forest of the RNI d'Andohahela (parcel 2) within the floristic zone known as the Mandrare Valley (Koechlin et al., 1974), located 7.5 km ENE of the village of Hazofotsy, 24°49.0'S, 46°36.6'E, at 120 m. Ten linear transects, each measuring 50 × 2 m (=0.01 ha) were installed. Trees, shrubs, and lianas with dbh ≥ 2.5 cm and rooted within the transect were censused, and their height was estimated from the ground (Gentry, 1982). Voucher specimens of fertile plants were collected for later species confirmation in the herbaria of PBZT and DRFP, Antananarivo. Two duplicates of nonfertile plants were also collected for comparison. Species of trees with dbh < 2.5 cm, understory trees, and herbaceous plants were identified, and if fertile, a herbarium specimen was preserved. General col-

lecting was also conducted within the surroundings of the transects, as well as within the gallery forest along the Mananara River, in order to estimate the diversity of the local flora and to provide a list of species occurring in the parcel.

Data Analysis

Although different survey techniques were employed in parcels 1 and 2, in many cases the variables measured for each of these techniques were identical. In cases where differences occurred, these are explained below.

The plot and transect studies involved several variables recorded in the field: the number of trees, their dbh and estimated height, and the number of species in each family. The relation between dbh and height was analyzed (for plots only). Furthermore, the biovolume (for plots only), density, basal area, relative dominance at specific and familial level, species diversity, and species frequency were calculated. Species accumulation curves as a function of area sampled were also plotted.

DISTRIBUTION OF DBH—The distribution of dbh classes was divided into increments of 5 cm for the plots and 2.5 cm for the transects.

HEIGHT DISTRIBUTION—Height distribution in intervals of 5 m was analyzed for each of the five plots as well as for the transects.

RELATION BETWEEN DBH AND HEIGHT—The relation of these two parameters was selected because they characterize the physiognomy of tropical forest. According to Hallé et al. (1978), the linear relationship between these two variables is $h = 100 \text{ dbh}$.

This model was proposed by Hallé et al. (1978) based on data from a Guyanese forest. A natural divergence from the proportion 1:100 is possible, particularly in Malagasy forests with a different flora and structure, and it could be the result of local natural factors rather than human perturbation. This relation provides a potentially useful comparison among the five plots along the elevational transect in parcel 1.

ESTIMATION OF BIOVOLUME—Biovolume, expressed in m^3 , corresponds to an estimation of the wood volume of trees in a given area. In this study, it is calculated for trees with a dbh ≥ 10 cm in the five 1 ha plots. This value was calculated in two different ways, using the biomass calculations of Devineau (1984) and those of Lieberman et al. (1996). We have presented our re-

sults using both formulas, hereafter termed biovolume a and biovolume b (respectively), in order to allow broader comparisons with other published works.

DENSITY—The density measure, used in both the plots and the transects, estimates the number of individuals of a given taxon found in a fixed area (Curtis & McIntosh, 1950).

BASAL AREA AND RELATIVE DOMINANCE—Using dbh, the basal area can be calculated for each tree for both the plots and transects (CTF, 1989). The dominance value for a given taxon provides information on the importance of that taxon by considering the area it occupies over the total area studied (Mori et al., 1983).

FREQUENCY—Each plot was divided into a fixed number of sampling units, whereas each of the 10 linear transects measured in parcel 2 represented a single sampling unit. The frequency of a taxon corresponds to the number of units in which it is found. This is usually calculated for species (Curtis & McIntosh, 1950).

RELATIVE SPECIES DIVERSITY PER FAMILY—The species diversity per family is the number of species counted of a given family in a delimited area (Curtis & McIntosh, 1950).

SPECIES-AREA CURVE—A species-area curve represents the cumulative number of species (including morphospecies) previously unrecorded at the site in relation to increasing sample area. If the curve reaches a plateau, then the studied area is representative of the flora within the local habitat. Further, based on the shape of the curve, it is also possible to estimate how homogeneous the site is with regard to species representation (Hill et al., 1994).

FAMILY IMPORTANCE VALUE—A family importance value (FIV) index establishes the importance of a family with respect to others, considering three factors: the abundance (density), the basal area (dominance), and the species diversity (Mori et al., 1983).

IMPORTANCE VALUE INDEX—A species importance value index (IVI) allows an evaluation of diversity at the species level, considering three factors: the abundance (density), the basal area (dominance), and the frequency (Curtis & McIntosh, 1950). This index has been criticized by Spurr (1964) and Silva (1980), who have pointed out that in tropical forests relative frequency and relative density are often nearly equal, and therefore the index does not give enough weight to tree size. However, Schulz (1960, pp. 160–161) demonstrated the problem of placing too much value

TABLE 4-1. Measured general parameters for 1 ha plots at five different sites in parcel 1 of the RNI d'Andohahela.

Plot	Altitude (m)	Number of trees having a dbh ≥10 cm	Mean dbh (cm)	Mean height (m)	Basal area (m ²)	Bio- volume a (m ³)	Bio- volume b (m ³)	Number of families	Number of species
1	440	739	20.5 ± 0.9	14.4 ± 0.6	34.1	270	160	31	121
2	840	880	20.9 ± 1.6	13.5 ± 0.9	43.2	430	260	34	146
3	1150	1,216	18.8 ± 0.6	13.8 ± 0.3	43.8	440	270	38	126
4	1550	675	24.4 ± 1.9	14.3 ± 0.4	63.8	740	450	26	65
5	1875	1,365	21.8 ± 1.0	10.1 ± 0.2	65.9	430	260	23	50

on basal area as an indicator of importance. In this report, we employ the IVI to allow broader comparisons.

A DIVERSITY INDEX, THE SHANNON-WEAVER INDEX—Species diversity, a characteristic of biological organization at the community level, provides a measure of community structure. In this survey, we chose to use the Shannon-Weaver diversity index, H' (Shannon & Weaver, 1949). Indeed, if measures of species abundance other than counts are used, only the Shannon-Weaver formula is available (Greig-Smith, 1983). Such a sample will not contain representatives of each species in the entire community. However, the absence of rare species has little effect on the value of H' (Brower et al., 1990).

A SIMILARITY INDEX, THE HORN INDEX—After tabulating the species composition of each of the five 1 ha plots studied, one of several approaches can be used to assess how similar they are to each other. We chose the index of community similarity proposed by Horn, which is derived from the Shannon-Weaver diversity index (Brower et al., 1990). The Horn index, R_0 , was calculated at the species and family levels for FIV and IVI figures derived from the plots (Goldsmith et al., 1986).

Results

Part I: The Humid Forest of Parcel 1

Data Analysis

Structural Parameters

Table 4-1 summarizes the number of trees recorded in each plot having a dbh ≥10 cm, the mean dbh, the mean height, the total basal area,

the values for biovolume a and biovolume b, the number of families, and the number of species.

NUMBER OF TREES AND BASAL AREA—The number of trees increased along the elevation gradient, with the exception at 1550 m, where the lowest density was noted. The lowest total basal area was observed in plot 1 at 440 m. Plot 3 at 1150 m had about 30% more trees than plot 2 at 840 m, although the basal areas in both plots were nearly equivalent. The number of trees was about 100% greater at 1875 m than at 1550 m, but the basal areas in both of these plots were similar. Even though the number of trees was lower at 1550 m than in the adjacent plots, the total basal area was much higher at 1550 m and 1875 m than at 1150 m. Thus, the number of trees and the basal area must be considered together.

DISTRIBUTION OF DBH—Table 4-2 presents information on the distribution of dbh for each plot; this is graphically presented in Figure 4-1. The majority of trees in the plots had dbh <20 cm, with percentages of 63.1% at 440 m, 65.4% at 840 m, 69.1% at 1150 m, 54.9% at 1550 m, and 54.7% at 1875 m. Few individuals had dbh values ≥50 cm. The principal families with individuals having large dbh values were Elaeocarpaceae, Lauraceae, Monimiaceae, Moraceae, Myrtaceae, and Sapotaceae. Within each plot the distribution of dbh had an inverted J-shape curve, which is characteristic of primary forest (Mori & Boom, 1987).

HEIGHT DISTRIBUTION—Table 4-3 presents data on the distribution of tree height measured in each plot. There were few trees exceeding 25 m in height and almost none taller than 30 m. The only trees having a dbh ≥10 cm and a height <10 m were found at 1875 m; in this elevational zone the mean height was distinctly lower than in all the other plots (Table 4-1). By setting the lower limit for dbh measurements at 10 cm, a large proportion of the trees <10 m in height were not sam-

TABLE 4-2. Distribution of dbh for the measured trees in each plot.

Plot	dbh (cm)									
	10-15	15-20	20-25	25-30	30-35	35-40	40-45	45-50	50-80	80-100
440 m	311 (42.1%)	155 (21.0%)	99 (13.4%)	60 (8.1%)	41 (5.6%)	23 (3.1%)	14 (1.9%)	10 (1.4%)	14 (1.9%)	4 (0.5%)
840 m	374 (44.0%)	182 (21.4%)	105 (12.3%)	61 (7.2%)	33 (3.9%)	32 (3.8%)	22 (2.6%)	10 (1.2%)	19 (2.2%)	8 (0.9%)
1150 m	570 (46.9%)	270 (22.2%)	161 (13.2%)	88 (7.2%)	43 (3.5%)	34 (2.8%)	21 (1.7%)	13 (1.1%)	16 (1.3%)	0 (0.0%)
1550 m	225 (33.3%)	146 (21.6%)	109 (16.2%)	49 (7.3%)	41 (6.1%)	24 (3.6%)	17 (2.5%)	15 (2.2%)	36 (5.3%)	6 (0.9%)
1875 m	474 (34.4%)	279 (20.3%)	209 (15.2%)	129 (9.4%)	120 (8.7%)	62 (4.5%)	30 (2.2%)	20 (1.5%)	40 (2.9%)	2 (0.2%)

Note: The total number of individuals may be lower than that presented in Table 4-1 because of the loss of some values.

pled. If every tree had been considered without regard to dbh value, an inverted J-shape curve of height distribution would probably have been observed.

RELATION BETWEEN DBH AND HEIGHT—As noted above, Hallé et al. (1978) hypothesized that a standard relation exists between dbh and tree height according to the formula $h = 100 \text{ dbh}$. The relationships of the linear regressions obtained for the five plots in parcel 1 (Table 4-4) are markedly different from those discussed by Hallé et al. (1978). The values are similar for the 440, 840, and 1150 m zones, whereas those at 1550 and 1875 m strongly deviate from expected values. The latter two sites have already been shown to be distinct from the lower three zones with regard to dbh and height. On the basis of the relation presented by Hallé et al. (1978), the humid forest of the RNI d'Andohahela does not fit their equation, and it might be construed that this forest is in an unbalanced state (i.e., not primary). We know this not to be the case, and a more reasonable interpretation would be that their relation is not valid for all types of humid forests. A larger study extended to a numerous forests on the island and multiple samples could clarify this point. Furthermore, such a study would also allow assessment of possible constant h/dbh ratios for different forest types and the effect of elevational variation.

Floristic Parameters

The five most important families in terms of relative density, relative dominance, relative species diversity, and FIV for each plot are given in Table 4-5 and graphically presented in Figure 4-2. A more detailed listing of the families recorded in each plot is given in Appendix 4-3.

Regarding relative density, relative dominance, relative frequency, and IVI, the 10 most important species in each plot are presented in Table 4-6 and Figure 4-3. A complete listing for these parameters is given in Appendix 4-4.

The number of species representing various percentages of cumulative density is a useful indication of the species diversity (Rollet, 1983; Johnston & Gillman, 1995). Table 4-7 presents the number of species with their respective percentage of the total number of species present in the plot, which comprised the first 25%, 50%, 75%, and 95% of the total relative density for each plot. No plant family or species dominated all five

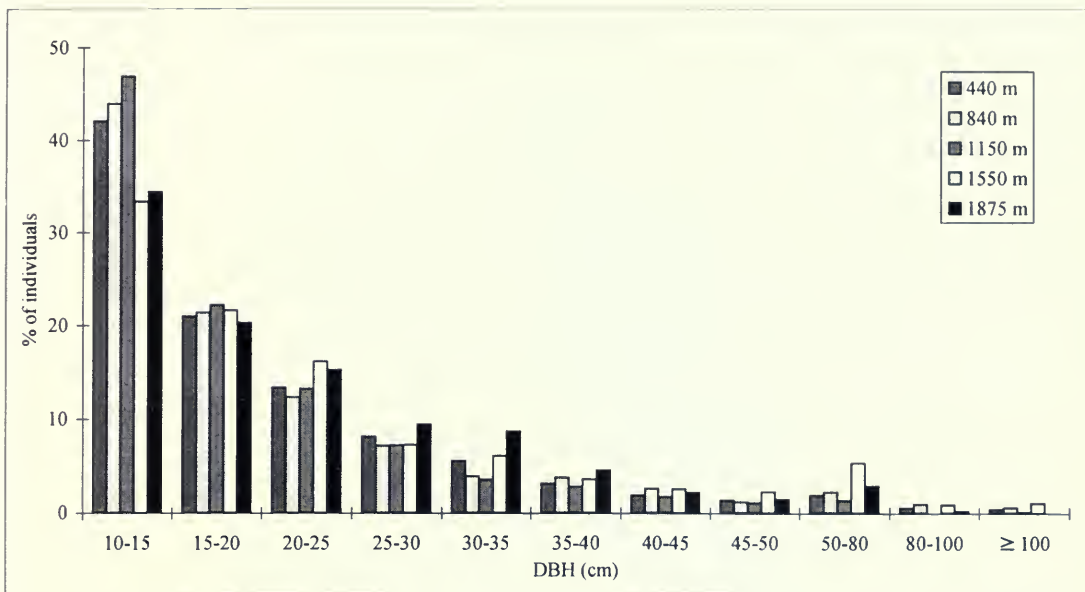


FIG. 4-1. Distribution of dbh measurements taken in the five 1 ha study plots in parcel 1 of the RNI d'Andohahela.

study plots, although a few families and a few species represented the first 50% of density in each plot. The percentage of species that represented half of the total density is lowest in the 1550 m plot (9%) and highest in the 1875 m plot (18%). These patterns are correlated with the high values of FIV and IVI in the 1550 m plot (Appendices 4-3 and 4-4).

In parcel 1 of the RNI d'Andohahela Lauraceae was well represented in every elevational zone on the basis of abundance, basal area, and species diversity. This family, as well as the Myrtaceae, was dominant at the higher altitudinal levels. *Weinmannia* (Cunoniaceae), a genus typical of high altitudes, was common in the 1550 and 1875 m plots; a few individuals were sampled as low as 840 m. Elaeocarpaceae, represented by the enormous *Sloanea rhodantha*, was an important

family with regard to basal area. Even if the species diversity of Elaeocarpaceae was low, this family includes most of the emergents, especially at higher elevations. *Chrysophyllum boivinianum* was mainly observed at 440 m; individuals were still present at 840 m. This tree is typical of lowland forests, where it is often one of the largest emergents. *Tambourissa* spp. (Monimiaceae) were very common from 440 to 1150 m. At 1550 and 1875 m Monimiaceae were uncommon; only six small individuals of *Tambourissa* were encountered at 1550 m, and species of *Ehippiandra* are seen at the higher altitudes. Many *Oncostemum* spp. (Myrsinaceae) were counted at 440 m. This is one of the dominant trees of lowland forest but becomes less frequent with increasing elevation. Many individuals of *Dombeya* (Sterculiaceae) and *Macaranga* (Euphorbiaceae) were

TABLE 4-3. Distribution of height classes for the measured trees in each plot.

Plot	Height (m)						
	0–5	5–10	10–15	15–20	20–25	25–30	≥30
440 m	0 (0.0%)	0 (0.0%)	260 (35.2%)	163 (22.1%)	71 (9.6%)	7 (1.0%)	0 (0.0%)
840 m	0 (0.0%)	0 (0.0%)	309 (36.3%)	233 (27.4%)	80 (9.4%)	43 (5.1%)	1 (0.1%)
1150 m	0 (0.0%)	0 (0.0%)	446 (35.9%)	307 (24.7%)	157 (12.6%)	20 (1.6%)	0 (0.0%)
1550 m	0 (0.0%)	0 (0.0%)	180 (26.7%)	215 (31.9%)	77 (11.4%)	26 (3.9%)	0 (0.0%)
1875 m	20 (1.5%)	523 (38.3%)	745 (54.7%)	75 (5.5%)	0 (0.0%)	0 (0.0%)	0 (0.0%)

Note: The total number of individuals may be lower than that presented in Table 4-1 because of the loss of some values.

TABLE 4-4. Relationship between height and dbh, with the respective r^2 value.

Plot	Altitude	Linear regression equation	r^2
1	440 m	$h = 55.8 \text{ dbh}$	-0.31
2	840 m	$h = 50.8 \text{ dbh}$	-0.58
3	1150 m	$h = 60.4 \text{ dbh}$	-0.51
4	1550 m	$h = 33.7 \text{ dbh}$	-2.75
5	1875 m	$h = 40.0 \text{ dbh}$	-1.10

present in the 1150 and 1550 m plots. These two genera contain colonizing species of trees, and in each of these plots there was an open area in which these trees were concentrated.

AREA-SPECIES CURVE—The species accumulation curves for all five 1 ha plots are presented in Figure 4-4. The curves for the three lowest elevations, 440, 840, and 1150 m, reflect a relatively homogeneous vegetation within each plot. The curves are gradual, although the study areas were not large enough to include the majority of species in the immediate local habitat. In contrast, the number of species occurring in the 1550 and 1875 m plots is distinctly smaller and a near plateau is reached in the species accumulation curves. This presumably also reflects a reduced botanical diversity as compared to the three lower elevational

zones. In general it would appear that the species sampled in the 1550 and 1875 m 1 ha plots are probably more representative of the local floral communities within these zones than the plots at lower elevation. A single 1 ha plot, or perhaps a plot as small as 0.5 ha, at upper elevations may have been sufficient to characterize the local vegetational communities. As a final point to this section, we note that species-area curves may vary depending on the site chosen for the plot, owing to the spatial distribution of species (Fangliang et al., 1996). In some of our plots it was clear that certain species showed a clump distribution.

THE SHANNON-WEAVER DIVERSITY INDEX—Within the 1 ha plots sampled, the highest Shannon-Weaver diversity index value was at 840 m, closely followed by that at the 1150 m plot, and finally by that at the 440 m plot (Table 4-8). The lowest diversity index values were observed at the 1550 and 1875 m plots. There was no clear difference between the various index values for the 440 and 840 m plots. Furthermore, because the ratios of the number of species to the number of individuals were similar between these two elevational zones, the number of trees sampled has to be considered. The high diversity index at 1150 and 1875 m is explained by the high number of sampled trees. Indeed, when considering the ratio

TABLE 4-5. Listing of the five most important families for four parameters in each 1 ha plot.

	Plot 1, 440 m	Plot 2, 840 m	Plot 3, 1150 m	Plot 4, 1550 m	Plot 5, 1875 m
Relative density	Rubiaceae Clusiaceae Lauraceae Myrsinaceae Monimiaceae	Monimiaceae Moraceae Myrtaceae Euphorbiaceae Araliaceae	Myrtaceae Lauraceae Sterculiaceae Moraceae Monimiaceae	Euphorbiaceae Lauraceae Sterculiaceae Monimiaceae Cunoniaceae	Araliaceae Lauraceae Myrtaceae Clusiaceae Flacourtiaceae
Relative dominance	Elaeocarpaceae Clusiaceae Sapotaceae Rubiaceae Lauraceae	Elaeocarpaceae Moraceae Myrtaceae Lauraceae Flacourtiaceae	Lauraceae Sterculiaceae Myrtaceae Monimiaceae Moraceae	Elaeocarpaceae Monimiaceae Lauraceae Sterculiaceae Euphorbiaceae	Araliaceae Lauraceae Cunoniaceae Elaeocarpaceae Flacourtiaceae
Relative species diversity	Rubiaceae Lauraceae Clusiaceae Myrsinaceae Euphorbiaceae	Moraceae Clusiaceae Rubiaceae Lauraceae Monimiaceae	Rubiaceae Euphorbiaceae Lauraceae Myrtaceae Moraceae	Lauraceae Sterculiaceae Rubiaceae Monimiaceae Clusiaceae	Lauraceae Myrtaceae Rubiaceae Araliaceae Cunoniaceae
FIV	Rubiaceae Clusiaceae Lauraceae Elaeocarpaceae Myrsinaceae	Moraceae Elaeocarpaceae Monimiaceae Myrtaceae Rubiaceae	Lauraceae Myrtaceae Sterculiaceae Moraceae Rubiaceae	Elaeocarpaceae Lauraceae Sterculiaceae Euphorbiaceae Monimiaceae	Lauraceae Araliaceae Myrtaceae Cunoniaceae Elaeocarpaceae

FIV, family importance value (index).

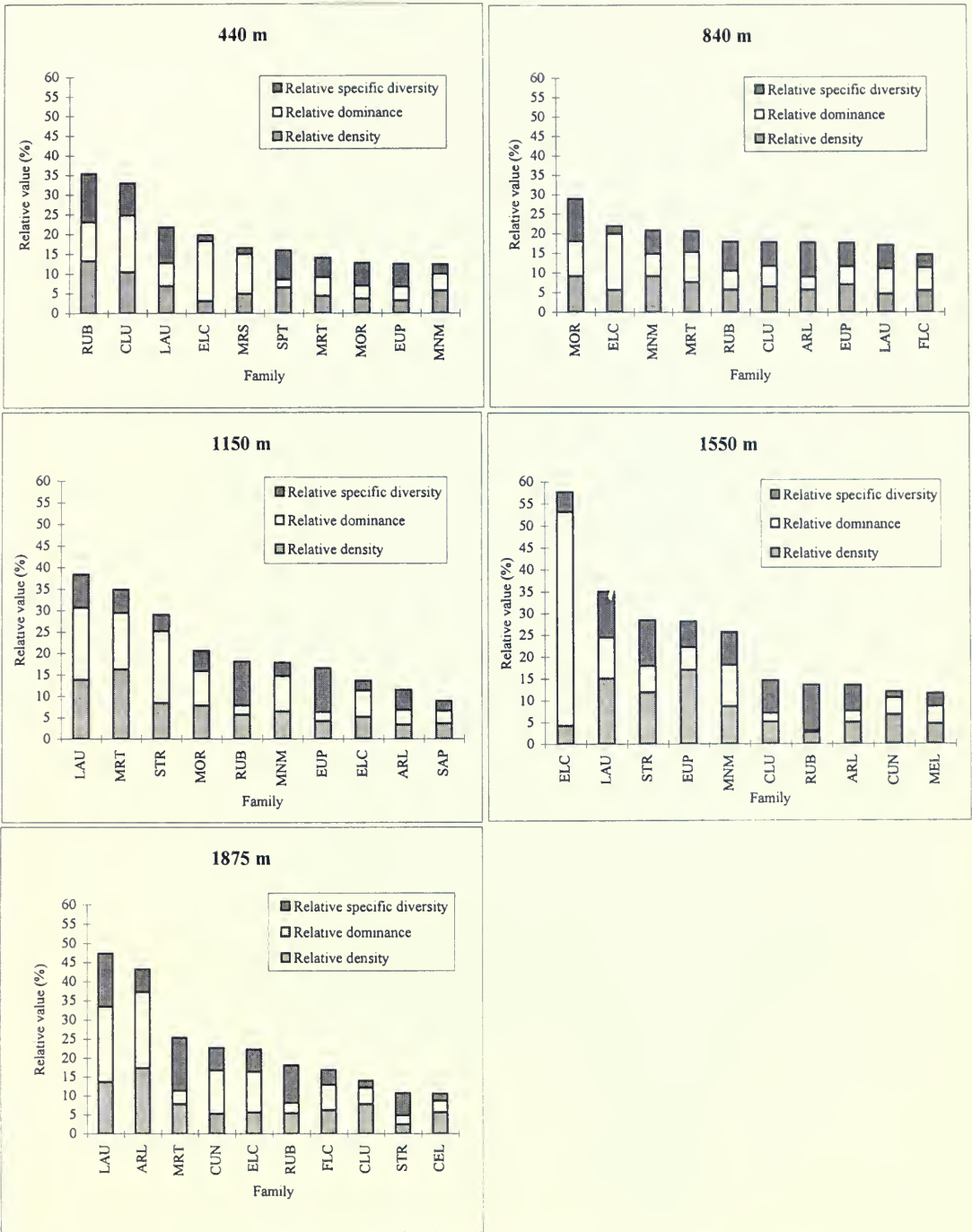


FIG. 4-2. Relative density, relative dominance, relative species diversity, and FIV for the five 1 ha study plots in parcel 1 of the RNI d'Andohahela. Each plot is presented separately. Abbreviations refer to families: ARL, Araliaceae; CEL, Celastraceae; CLU, Clusiaceae; CUN, Cunoniaceae; ELC, Elaeocarpaceae; EUP, Euphorbiaceae; FLC, Flacourtiaceae; LAU, Lauraceae; MEL, Meliaceae; MNM, Monimiaceae; MOR, Moraceae; MRS, Myrsinaceae; MRT, Myrtaceae; RUB, Rubiaceae; SAP, Sapindaceae; SPT, Sapotaceae; and STR, Sterculiaceae.

TABLE 4-6. Listing of the 10 most important species for four parameters in each 1 ha plot.

	Plot 1, 440 m	Plot 2, 840 m	Plot 3, 1150 m	Plot 4, 1550 m	Plot 5, 1875 m
1 Relative density					
2	<i>Mammea</i> sp3 <i>Sorindeia</i> <i>madagascariensis</i>	<i>Sloanea rhodantha</i> var. <i>rhodantha</i> <i>Macaranga</i> sp1 <i>Sreblus dinepate</i>	Myrtaceae sp13 <i>Trilepistum</i> <i>madagascariensis</i>	<i>Macaranga</i> sp2 Lauraceae sp10 <i>Weinmannia</i> sp4 <i>Cyathia</i> spp.	<i>Polyscias</i> sp7 <i>Garcinia</i> sp2 <i>Brexiella</i> sp1 <i>Polyscias</i> sp9 <i>Aplioia theaeformis</i> <i>Belschmedia</i> sp1 <i>Ilex mitis</i>
3	<i>Ilex mitis</i>	<i>Myrtaceae</i> sp11	Myrtaceae sp14	Myrtaceae sp10	<i>Polyscias</i> sp9
4	<i>Tambourissa</i> sp2	<i>Polyscias</i> sp1	Lauraceae sp10	<i>Mallectastrum</i> sp1	<i>Aplioia theaeformis</i>
5	<i>Dracaena reflexa</i>	<i>Tambourissa</i> sp1	<i>Tambourissa</i> sp7	<i>Mallectastrum</i> sp1	<i>Belschmedia</i> sp1
6	<i>Chrysophyllum</i> <i>boivinianum</i>	Flacourtiaceae sp1	<i>Dombeya</i> sp9	<i>Dombeya</i> sp2	<i>Ilex mitis</i>
7	<i>Hyperacanthus</i> sp1	<i>Ophiocolea floribunda</i>	<i>Sloanea rhodantha</i>	<i>Polyscias</i> sp9	<i>Ephippiandra</i> sp1
8	Lauraceae sp3	<i>Tambourissa</i> sp2	var. <i>rhodantha</i>	<i>Sloanea rhodantha</i>	<i>Cryptocarya</i> sp3
9	<i>Oncostemum</i> sp2	<i>Ocotea</i> sp1	<i>Dombeya</i> sp3	var. <i>rhodantha</i>	<i>Sloanea rhodantha</i>
10	Myrtaceae sp7		<i>Allophyllus</i> sp2 <i>Ilex mitis</i>	Lauraceae sp15	var. <i>quercifolia</i>
11 Relative dominance					
12	<i>Sloanea rhodantha</i> var. <i>rhodantha</i> <i>Chrysophyllum</i> <i>boivinianum</i>	<i>Sloanea rhodantha</i> var. <i>rhodantha</i> Moraceae sp1 Annonaceae sp1 <i>Ocotea</i> sp1	<i>Dombeya</i> sp9 <i>Tambourissa</i> sp4 Myrtaceae sp14	<i>Sloanea rhodantha</i> var. <i>quercifolia</i> <i>Sloanea rhodantha</i> var. <i>rhodantha</i>	<i>Polyscias</i> sp7 <i>Weinmannia</i> sp4 <i>Belschmedia</i> sp1 <i>Sloanea rhodantha</i> var. <i>quercifolia</i>
13	<i>Mammea</i> sp3	<i>Polyscias</i> sp1	<i>Sloanea rhodantha</i>	Monimiaceae sp1	<i>Aplioia theaeformis</i>
14	<i>Ilex mitis</i>	<i>Weinmannia</i> sp5	var. <i>rhodantha</i>	<i>Macaranga</i> sp2	<i>Garcinia</i> sp2
15	Lauraceae sp2	Myrtaceae sp11	Lauraceae sp10	<i>Mallectastrum</i> sp1	<i>Ilex mitis</i>
16	Lauraceae sp3	Myrtaceae sp1	<i>Trilepistum</i>	<i>Weinmannia</i> sp4	<i>Aguardia</i> sp1
17	<i>Plagioscyphus</i> sp2	Myrtaceae sp1	<i>madagascariensis</i>	Lauraceae sp15	Lauraceae sp16
18	<i>Hyperacanthus</i> sp1	<i>Diospyros</i> sp3	<i>Ilex mitis</i>	Lauraceae sp10	<i>Cryptocarya</i> sp3
19	Rubiaceae sp2	<i>Tisonia</i> sp1	<i>Chrysophyllum</i> <i>boivinianum</i>	<i>Tambourissa</i> sp1	
20	<i>Dracaena reflexa</i>		<i>Dombeya</i> sp3	<i>Polyscias</i> sp9	
21 Relative frequency					
22	<i>Ilex mitis</i> <i>Sorindeia</i> <i>madagascariensis</i>	<i>Sloanea rhodantha</i> var. <i>rhodantha</i> <i>Sreblus dinepate</i>	Myrtaceae sp14 Myrtaceae sp13	<i>Macaranga</i> sp2 Monimiaceae sp1	<i>Polyscias</i> sp7 <i>Garcinia</i> sp2
23	<i>Hyperacanthus</i> sp1	Myrtaceae sp11	<i>Dombeya</i> sp3	Lauraceae sp10	<i>Aplioia theaeformis</i>
24	<i>Dracaena reflexa</i>	<i>Polyscias</i> sp1	<i>Sloanea rhodantha</i>	<i>Weinmannia</i> sp4	<i>Polyscias</i> sp9
25	Lauraceae sp3	<i>Tambourissa</i> sp1	var. <i>rhodantha</i>	<i>Cyathia</i> spp.	<i>Belschmedia</i> sp1
26	<i>Mammea</i> sp3	<i>Ophiocolea floribunda</i>	<i>Allophyllus</i> sp2	<i>Sloanea rhodantha</i>	<i>Cryptocarya</i> sp3
27	<i>Tambourissa</i> sp2	Flacourtiaceae sp1	Lauraceae sp10	var. <i>rhodantha</i>	<i>Sloanea rhodantha</i>
28	<i>Chrysophyllum</i> <i>boivinianum</i>	<i>Ocotea</i> sp1	<i>Tambourissa</i> sp7	<i>Mallectastrum</i> sp1	var. <i>quercifolia</i>
29	<i>Oncostemum</i> sp2	<i>Tambourissa</i> sp2	<i>Trilepistum</i>	<i>Dombeya</i> sp2	<i>Brexiella</i> sp1
30	Moraceae sp1	<i>Ilex mitis</i>	<i>madagascariensis</i> <i>Ilex mitis</i>	Lauraceae sp15	<i>Ephippiandra</i> sp1
			Lauraceae sp9	<i>Polyscias</i> sp8	Rubiaceae sp1

TABLE 4-6. Continued.

	Plot 1, 440 m	Plot 2, 840 m	Plot 3, 1150 m	Plot 4, 1550 m	Plot 5, 1875 m
31 IVI	<i>Mammea</i> sp3	<i>Sloanea rhodantha</i>	<i>Dombeya</i> sp9	<i>Sloanea rhodantha</i>	<i>Polyscias</i> sp7
32	<i>Chrysophyllum boivinianum</i>	var. <i>rhodantha</i>	Myrtaceae sp13	var. <i>quercifolia</i>	<i>Garcinia</i> sp2
33	<i>Sloanea rhodantha</i> var. <i>rhodantha</i>	<i>Polyscias</i> sp1	Myrtaceae sp14	<i>Macaranga</i> sp2	<i>Belshamedia</i> sp1
34	<i>Ilex mitis</i>	<i>Ocotea</i> sp1	<i>Trilepisium madagascariensis</i>	<i>Sloanea rhodantha</i> var. <i>rhodantha</i>	<i>Aphloia theaeformis</i>
35	<i>Tambourissa</i> sp2	<i>Streblus dimorpha</i>	Lauraceae sp10	Lauraceae sp10	var. <i>quercifolia</i>
36	<i>Sorindeia madagascariensis</i>	Moraceae sp1	<i>Sloanea rhodantha</i> var. <i>rhodantha</i>	Monimiaceae sp1	<i>Weinmannia</i> sp4
37	<i>Dracaena reflexa</i>	<i>Macaranga</i> sp1	<i>Dombeya</i> sp3	<i>Weinmannia</i> sp4	<i>Polyscias</i> sp9
38	Lauraceae sp3	<i>Tambourissa</i> sp1	<i>Tambourissa</i> sp7	<i>Malteastrum</i> sp1	<i>Brexiella</i> sp1
39	<i>Hyperacanthus</i> sp1	<i>Ophiocolea floribunda</i>	<i>Ilex mitis</i>	<i>Cyathea</i> spp.	<i>Ilex mitis</i>
40	<i>Oncostemum</i> sp2	<i>Tambourissa</i> sp2	<i>Tambourissa</i> sp4	Lauraceae sp15	<i>Cryptocarya</i> sp3
				<i>Dombeya</i> sp2	

IVI, importance value index.

of the number of species to the number of individuals, the 1150 m plot is clearly less diverse than the plots at 440 and 840 m, but it is very similar to that at 1550 m. The plot below the summit at 1875 m had a proportionately lower diversity than the other plots.

The Shannon-Weaver diversity index values for the five plots are relatively very low, falling between 1.49 and 1.86. This is due to the dominance of some species in each plot. For example, the 1550 m plot had the lowest Shannon-Weaver diversity index value, and *Macaranga* sp2 represented 14.07% of the total tree density. Indeed, the Shannon-Weaver diversity index strongly weighs the number of species and the relative density of each species. The low diversity index is the result of the small number of species that account for over 50% of the number of trees in the various size classes; individual species and family dominance within low-diversity forests is high.

THE HORN SIMILARITY INDEX—Dendrograms showing the degree of similarity in family and species composition between each plot on the basis of the FIV and IVI are presented in Figure 4-5. These dendrograms corroborate our earlier interpretations of the floristic relationships between the various elevational zones.

Discussion

The eastern Malagasy humid forest contains a number of distinct vegetational communities that vary as a function of altitude. According to Humbert and Cours Darne (1965) and Koechlin et al. (1974), lowland rain forest reaches up to 800 m and is characterized by the presence of *Sloanea rhodantha*, *Canarium madagascariense*, Myristicaceae, and *Anthostema* (Euphorbiaceae). The mid-altitude moist forest, occurring between 800 and 1800 m, is distinguished by *Weinmannia* (Cunoniaceae), *Tambourissa* (Monimiaceae), *Symphonia* (Clusiaceae), *Ravensara*, and *Ocotea* (Lauraceae), as well as *Canarium madagascariense*. Finally, they described a stratum between 1800 and 2000 m composed of moist montane forest. Podocarpaceae and *Weinmannia* are two of the taxa characterizing this latter formation.

On the basis of the above classification, plots 1 (440 m) and 2 (840 m) would belong to the lowland rain forest; the upper elevational limit of this zone is subject to some variation and may reach

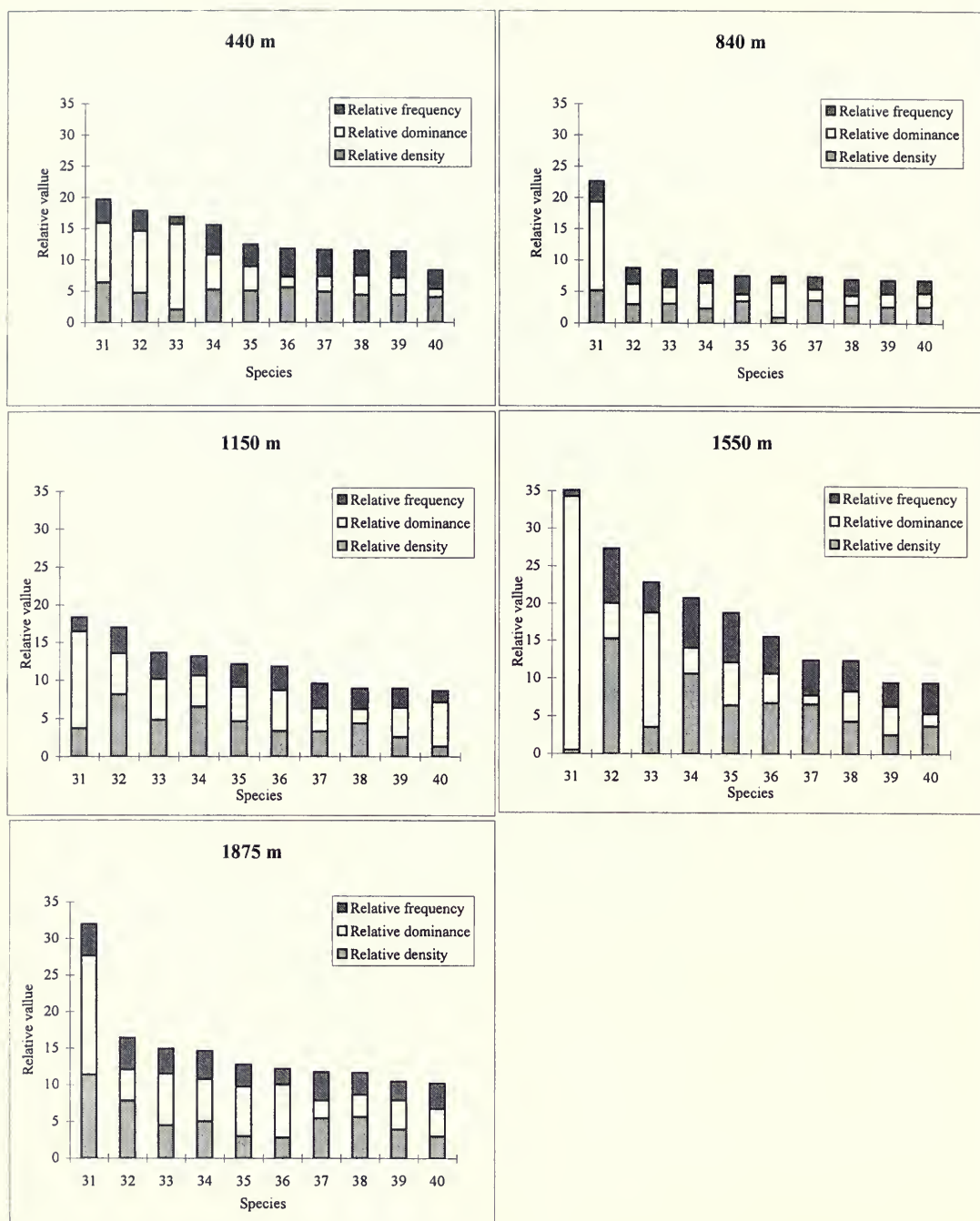


FIG. 4-3. Relative density, relative dominance, relative frequency, and IVI for the five 1 ha study plots in parcel 1 of the RNI d'Andohabeha. Each plot is presented separately. The numbers correspond to those presented in Table 4-6.

TABLE 4-7. Number of species (n) with respective percentage (%) representing the indicated percentage (25%, 50%, 75%, 95%) of the total relative density.

Plot	Altitude (m)	Relative density							
		25%		50%		75%		95%	
		n	%	n	%	n	%	n	%
1	440	5	4	12	10	34	28	93	78
2	840	8	5	20	14	46	32	107	73
3	1150	4	3	13	10	30	24	81	64
4	1550	2	3	6	9	16	25	41	63
5	1875	3	6	9	18	19	38	37	74

higher elevations in some regions of the island (Lowry et al., 1997). Plots 3 (1150 m) and 4 (1550 m) fall within the range of mid-altitude moist forest, and plot 5, at 1875 m, is classified as moist montane forest. The taxonomic results obtained in the plots at 440 and 840 m are similar to one another (Table 4-5; Fig. 4-5) and corroborate the descriptions made by Humbert and Cours Darne (1965) and Koechlin et al. (1974). At 1550 m in the moist montane forest formation, *Weinmannia* was abundant, whereas it was completely absent in the 1150 m plot. *Tambourissa* was common at 1150 m and appeared to reach its upper limit at about 1200 m. Few *Symphonia* were counted in the plots at 1150 and 1550 m, but this genus was often noted during the general collecting in each of these zones. *Ocotea* and *Ravensara* were dominant at these two elevational

zones (Table 4-5). Finally, on the basis of elevation, the plot at 1875 m would fall into the upper zone of the moist montane forest. This plot had many similarities to those at lower elevations, but the presence of some taxa, particularly *Ericaceae*, attests that this site should be assigned to moist montane forest. This is particularly true at the species level, whereas at the family level it is very similar to the plot at 1550 m (Fig. 4-5).

One surprising observation was the absence or rarity of two often dominant families in Malagasy humid forest, *Podocarpaceae* and *Burseraceae* (*Canarium* spp.). No *Podocarpus* was found in any of the transect zones studied. This genus has been reported previously from Beampigaratra (Laubenfels, 1972), another region of the Anosyenne Mountains. Furthermore, at other sites such as the eastern slopes of the RNI

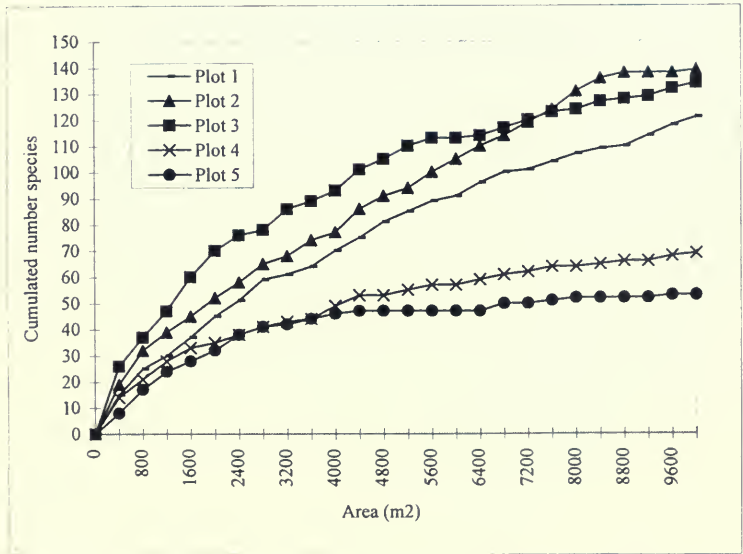


FIG. 4-4. Species accumulation curves for the 1 ha plots in five different elevational zones in parcel 1 of the RNI d'Andohahela.

TABLE 4-8. H' (Shannon-Weaver diversity index value) for each plot, using the number of individuals in each taxon.

Plot	Altitude (m)	Shannon-Weaver diversity index		Species : individual ratios
		Species	Families	
1	440	1.76	1.32	0.16
2	840	1.86	1.34	0.17
3	1150	1.77	1.29	0.11
4	1550	1.49	1.18	0.10
5	1875	1.52	1.21	0.04

d'Andringitra, *Podocarpus* was one of the dominant genera at 1600 m (Lewis et al., 1996). Similarly, in parcel 1 of the RNI d'Andohahela only four individuals of *Canarium* (Burseraceae) were counted in the plots, and even during general collecting members of this family were rare. Normally, *Canarium* is present in most Malagasy humid forests. This genus is cited by Humbert and Cours Darne (1965) as one of the characteristic emergent trees up to 1800 m. *Canarium* occurs as a large forest emergent, especially between 700 and 1000 m, in the RNI d'Andringitra (Lewis et al., 1996). In the RS de Manongarivo and the RNI

de Marojejy (Rakotomalaza & Messmer, pers. observ.) it is also a conspicuous member of the local plant community.

The latitudinal position of the RNI d'Andohahela could be a factor to explain this deviation from the accepted classification of plant zone indicators. The transect studied is situated south of the Tropic of Capricorn. The island of Madagascar spans 14 degrees of latitude, and climatic differences between the north and the south along the eastern coast have already been discussed by Donque (1972). According to Humbert and Cours Darne (1965) and Koechlin et al. (1974), their botanical classification with regard to vegetation composition or elevational is relatively constant. However, it appears that they did not consider a latitudinal gradient. One possibility would be that at such high latitudes as parcel 1, taxa descend to lower elevations. For example, Myristicaceae and *Anthostema* (Euphorbiaceae) are absent from the transect, but genera belonging to Myristicaceae were recorded at the same latitude at lower elevations outside of the reserve (Dumetz, 1993). Furthermore, *Canarium* might occur at elevations lower than 440 m, the lower limit of our parcel 1 study. This hypothesis is supported by the presence of *Chrysophyllum boivinianum*, *Ilex mitis*,

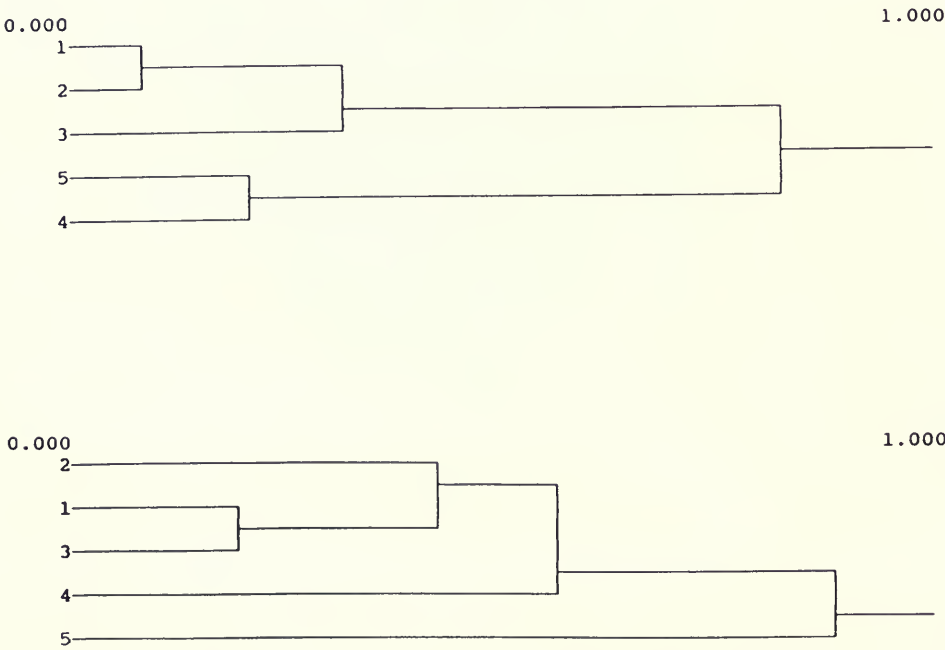


FIG. 4-5. Dendrograms (SYSTAT, version 2) using FIV data (top) and IVI data (bottom) for five different 1 ha plots in parcel 1 of the RNI d'Andohahela. The numbers along the left margin of the dendrograms represent the different plots.

and *Sloanea rhodantha* among the dominant species at 440 m, because these are all typically mid-elevation species and not known from low altitudes in forests further north (Schatz, 1994; Rabevohitra et al., 1996). In addition, few trees of the Proteaceae family, as represented by *Dilobeia thouarsii*, were found in the 440 and 840 m plots. This species was absent at higher altitudes, although it has been recorded up to 1800 m (Koechlin et al., 1974).

These observations support the hypothesis that the vegetation communities in parcel 1 of the RNI d'Andohahela exhibit a downward elevational shift. A few structural parameters also confirm this supposition. For example, canopy height was lower in plots at 440, 840, and 1150 m than is typical for these elevational zones elsewhere in Madagascar (Koechlin et al., 1974). Nevertheless, the 1550 and 1875 m plots had high values for density, basal area, and height. A decrease in tree height and dbh with altitude is expected (Koechlin et al., 1974). According to these two structural parameters, however, the plot at 1550 m is remarkable in comparison with the other plots; the number of trees having a dbh ≥ 50 cm was much higher than in the other plots, and it had the lowest value of trees with a diameter of < 20 cm. Even if the total density of the 1550 m plot was only nearly half that of the plot at 1150 m, the value of basal area had increased by nearly 50%. The distinctive aspects of the 1550 m plot were visually apparent during the field study.

The values of the structural data for parcel 1 of the RNI d'Andohahela are similar to those for other sites in Madagascar (Table 4-9). A broader comparison of the RNI d'Andohahela to forests studied in South America, Africa, and Asia indicates that the basal area values and the number of trees with stems ≥ 10 cm dbh are much higher along the elevational gradient in parcel 1 than at those other sites (Table 4-9). Family and species diversity indices are also much lower in the Andohahela plots than those calculated for forests in other parts of the tropics (Table 4-9). Thus, even if the numbers of families and species are similar between parcel 1 of the RNI d'Andohahela and those other forests, the number of trees for each of these taxonomical units is probably considerably different. The Shannon-Weaver diversity index considers the number of species and the number of individuals of each species. If a few species of trees have a much higher density than other sympatric species, the habitat is considered less diverse than one with the same number of species in which none is dominant. Along the transect in

the RNI d'Andohahela, the relative densities are unbalanced (Table 4-7). The habitats are thus less diverse in the sense of the Shannon-Weaver diversity index compared to other tropical forests.

Monimiaceae is a distinctive family of the Malagasy forests and not to the forests in the Neotropics, Asia, or Africa. Apart from the Dipterocarpaceae, which is a widespread and particular aspect of the forests of southeastern Asia, other dominant families occurring in this region and Madagascar are the same. They include, for example, Lauraceae, Myrtaceae, Elaeocarpaceae, and Clusiaceae (Gentry, 1988; Ohsawa, 1991; Kitayama, 1992; Pendry et al., 1997). Lauraceae is one of the dominant families, especially above 800 m, in most of the Malagasy humid forest (Schatz, 1994; Lewis et al., 1996; Rabevohitra et al., 1996), as well as in many other humid forests in other tropical regions (Johnston & Gillman, 1995; Kitayama, 1992; Pendry et al., 1997; Mori et al., 1983; Gentry, 1988; Ohsawa, 1991).

Legumes are virtually always the dominant family in Neotropical and African lowland primary forest, and their dominance in these regions is parallel to that of Dipterocarpaceae of southeastern Asia (Mori et al., 1983; Gentry, 1988; Lieberman et al., 1996). The major exception to this pattern is that legumes appear to be poorly represented among the woody plants with a dbh ≥ 10 cm in Malagasy humid forests (Schatz, 1994; Lewis et al., 1996; Rabevohitra et al., 1996). The scarcity of the Leguminosae is noticeable in parcel 1 of the RNI d'Andohahela; in the entire transect studied, only 35 trees out of a total of 4,875 (0.7%) belonged to this family.

Part II: The Spiny Forest of Parcel 2

Although several botanists, including pioneers such as Alluaud and Poisson (Poisson, 1912), have collected in the south of Madagascar, no quantitative data are available on spiny forest structure and floristic diversity; the only known exception is the study of Sussman and Rakotozafy (1994) in the RS de Beza Mahafaly.

Data Analysis

Structural Parameters

DISTRIBUTION OF DBH—Of the 607 individuals with a dbh ≥ 2.5 cm, 80% measured between 2.5

TABLE 4-9. Comparative data in other parts of the tropics.

Sites	Altitude (m)	Number of trees having a dbh ≥10 cm per ha	Basal area (m ²) per ha	Number of families	Number of species	Shannon- Weaver diversity index, families	Shannon- Weaver diversity index, species
Miaranony, Ranomafana, Madagascar (Lowry et al., 1997)	600	769	49.9	—	—	—	—
Vatoharanana, Ranomafana, Madagascar (Lowry et al., 1997)	950	660	35.0	—	—	—	—
Vohipara, Ranomafana, Madagascar (Lowry et al., 1997)	1200	1,092	25.6	—	—	—	—
Manombo, Madagascar (Rabevohitra et al., 1996)	80	787	—	38	119	—	—
Analava-Marovony, Madagascar (Dumetz, 1993)	50	1,200	—	—	—	—	4.90
	50	840	—	—	—	—	4.60
	50	940	—	—	—	—	4.70
	50	1,280	—	—	—	—	5.00
Manantantely, Madagascar (Dumetz, 1993)	250	900	—	—	—	—	3.90
	250	740	—	—	—	—	4.20
Bukit Belalong, Brunei (Pendry et al., 1997)	200	512	46.9	—	ca. 210	2.81	4.15
	500	663	51.1	—	ca. 230	2.76	4.22
	850	798	37.5	—	ca. 250	3.15	4.42
Mount Kinabalu, Borneo (Kitayama, 1992)	600	333	33.4	—	—	—	—
	800	372	29.8	—	—	—	—
	1000	369	27.5	—	—	—	—
	1200	447	34.0	—	—	—	—
	1400	759	46.6	—	—	—	—
	1600	572	33.2	—	—	—	—
	1800	593	39.0	—	—	—	—
	2000	497	36.7	—	—	—	—
Kurupukari, Guyana (Johnston & Gillmann, 1995)	Lowland	357	—	23	64	—	—
	Lowland	459	—	23	71	—	—
	Lowland	477	—	23	67	—	—
	Lowland	742	—	23	50	—	—
	Lowland	673	—	47	201	—	—
	Lowland	858	—	43	249	—	—
Cocha Cashu, Peru (Johnston & Gillmann, 1995)	Lowland	619	53.0	—	—	—	—
Mishana, Brazil (Johnston & Gillmann, 1995)	Lowland	540	34.8	—	—	—	—
La Fumée Mountain, French Guiana (Mori & Boom, 1987)	Lowland	492	39.3	—	—	—	—
Camaipi, Brazil (Mori & Boom, 1987)	Lowland	649	21.5	—	—	—	—
Rio Falsino, Brazil (Mori & Boom, 1987)	Lowland	728	36.1	—	—	—	—
Alto Ivon, Bolivia (Mori & Boom, 1987)	Lowland	891	46.3	—	—	—	—
Añagu, Ecuador (Mori & Boom, 1987)	Lowland						
Bahia, Brazil (Mori & Boom, 1987)	Lowland						

TABLE 4-9. *Continued.*

Sites	Altitude (m)	Number of trees having a dbh ≥10 cm per ha	Basal area (m ²) per ha	Number of families	Number of species	Shannon- Weaver diversity index, families	Shannon- Weaver diversity index, species
La Selva—Volcan Barva, Costa Rica (Lieberman et al., 1996)	300	551	26.4	55	149	3.42	4.51
	500	425	23.5	55	131	3.32	4.29
	750	565	30.3	50	125	3.21	4.19
	1000	535	27.4	41	100	3.16	4.10
	1250	610	23.1	36	82	2.63	3.63
	1500	571	26.2	37	74	2.96	3.76
Amazonian Ecuador (Balslev et al., 1987) Yanamono, Amazonian Peru (Gentry, 1988)	1750	479	28.2	33	64	2.87	3.61
	2000	477	28.6	32	55	2.86	3.46
	Lowland	728	33.7	53	228	—	—
	Lowland	606	—	48	300	—	—

and 10 cm, whereas only 2% measured ≥ 30 cm (Table 4-10; Fig. 4-6). These latter trees belonged to five species: *Operculicarya decaryi*, *Alluaudia ascendens*, *A. procera*, *Commiphora aprevalii*, and *Tetrapterocarpus geayi*. These species and other members of these genera are emergent trees. The only exception is *O. decaryi*, which is one of the region's characteristic bottle trees. The mean dbh of the measured trees was 7.42 ± 0.52 cm.

HEIGHT DISTRIBUTION—Of the 607 individual trees with a dbh ≥ 2.5 cm, 72% were between 0 and 5 m in height. Only 3.5% of the trees sampled had a height ≥ 10 m (Table 4-11; Fig. 4-7) and are represented by four species: *Alluaudia ascendens*, *A. procera*, *Commiphora marchandii*, and *Tetrapterocarpus geayi*. As noted above, the small trees making up the middle stratum had a height of about 2–4 m, and the canopy trees reached up to 5 or 6 m. The mean height of sampled trees was 4.18 ± 0.16 m.

Floristic Parameters

All of the floristic parameters are presented in Appendices 4-5 and 4-6.

DENSITY—A total of 10 linear transects were established in which 540 plants with dbh ≥ 2.5 cm were identified, belonging to 28 families and 78 species. Four families accounted for 50% of the individuals: Burseraceae (19.1%), Euphorbiaceae (13.3%), Didiereaceae (8.7%), and Ebenaceae (7.6%). The commonest species were *Gyrocarpus americanus* (Hernandiaceae); *Commiphora humbertii*, *C. aprevalii*, and *C. brevicalyx* (Burseraceae); *Alluaudia procera* (Didiereaceae); *Euphorbia intisy* (Euphorbiaceae); and *Diospyros humbertiana* (Ebenaceae).

BASAL AREA AND RELATIVE DOMINANCE—The total basal area was 4.5 m²; 0.45% of the study area (1,000 m²) contained trees having a dbh ≥ 2.5 cm. Half of the total basal area was occupied by only two families: Didiereaceae (two species of *Alluaudia*) accounted for 26.5% and Anacardiaceae (*Operculicarya decaryi*) accounted for 22.2%. Burseraceae, as represented by *Commiphora humbertii*, was the third most common family.

RELATIVE SPECIES DIVERSITY PER FAMILY—For the 0.1 ha study area, 78 species of trees, shrubs, and lianas with dbh ≥ 2.5 cm were sampled. Fabaceae was the most diverse family, with 10 species, followed by Euphorbiaceae. Didiereaceae,

TABLE 4-10. Distribution of dbh for the measured trees in the 10 transects in parcel 2 of the RNI d'Andohahela.

	dbh (cm)					
	2.5-5	5-10	10-15	15-20	20-25	25-30
n (%)	237 (39.4%)	239 (39.8%)	72 (12.0%)	13 (2.2%)	18 (3.0%)	10 (1.7%)
						≥30
						12 (2.0%)

Note: The total number of individuals is lower than that presented in the text because of the loss of some values.

Rubiaceae, and Burseraceae were represented by four, five, and six species, respectively.

FREQUENCY—Five species of *Commiphora*, two species of *Alluandia*, *Operculicarya decaryi*, one species of *Dichrostachys*, *Euphorbia onoclada*, and *Diospyros humbertiana* were the commonest censused trees and shrubs with a dbh ≥ 2.5 . The remaining taxa found in the study area occurred with more or less the same frequencies.

FAMILY IMPORTANCE VALUE (FIV) AND IMPORTANCE VALUE INDEX (IVI)—When the three factors of relative density, relative dominance, and relative species diversity are combined, the five most important families were Burseraceae, Didiereaceae, Euphorbiaceae, Anacardiaceae, and Fabaceae. When the three factors of relative density, relative dominance, and relative frequency are considered, the five most important species also belonged to these same families.

THE SHANNON-WEAVER DIVERSITY INDEX—The value of the Shannon-Weaver diversity index, H' , using species density data is 1.17. This is a very low value that is due to the dominance of a few species. In contrast, species richness, with 78 different species in 0.1 ha, is high.

Discussion

A total of 540 trees with dbh ≥ 2.5 cm were identified in the 0.1 ha study area. This included 78 species belonging to 28 families. When the lower limit of dbh was increased to ≥ 5 cm, the density of trees decreased to 364 per 0.1 ha and comprised 69 species. The mean value of the Shannon-Weaver diversity index is very low for trees with a dbh ≥ 2.5 cm; it can be accounted for by the dominance of a few species and the rarity of most species. Thus, in this case, even though the diversity value is low, in actuality the study area had a diverse flora.

The spiny forest of parcel 2 of the RNI d'Andohahela has a higher density and diversity than the spiny forest of Beza Mahafaly (Sussman & Rakotozafy, 1994). Because of differences in methodology only the following figures are comparable to our data: dbh ≥ 2.5 cm in 0.1 ha, 440 individuals; and dbh ≥ 2.5 cm in 0.25 ha, 69 species from 25 families (Sussman & Rakotozafy, 1994). The most common families were the same at both sites. The spiny forest of RNI d'Andohahela has also a higher tree density than

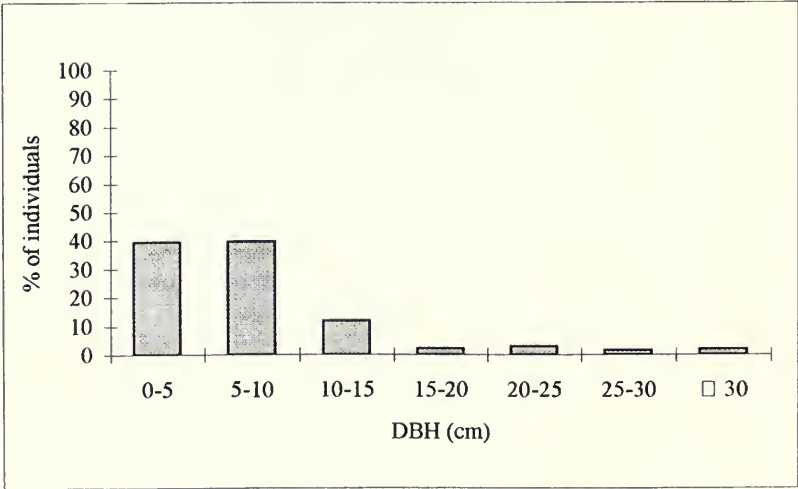


FIG. 4-6. Distribution of dbh measurements taken in the 10 transects in parcel 2 of the RNI d'Andohahela.

TABLE 4-11. Distribution of the height for the measured trees in the 10 transects in parcel 2 of the RNI d'Andohahela.

	Height (m)						
	0-2.5	2.5-5	5-7.5	7.5-10	10-12.5	12.5-15	≥15
n (%)	57 (10.4%)	339 (61.9%)	115 (21.0%)	18 (3.3%)	15 (2.7%)	3 (0.5%)	1 (0.2%)

Note: The total number of individuals is lower than that presented in the text because of the loss of some values.

dry forests in continental Africa and the Neotropics. Using the same transect method, Gentry (1993) found an average of 369 individuals ≥ 2.5 cm dbh/1,000 m² in a series of Neotropical lowland dry forests and 361 individuals in dry forests in Africa. In the El Pechiche dry forest of Ecuador, 57 trees with dbh ≥ 5 cm belonging to only 13 species were counted in 0.1 ha (Josse & Balslev, 1994). In western Ecuador, the total density of a 1 ha plot in a dry forest was 538 trees ≥ 5 cm dbh, and the total species richness was 37, belonging to 22 families. In the Paleotropical dry forest, Acanthaceae, Asclepiadaceae, Euphorbiaceae, and Tiliaceae were well represented (Thomasson & Thomasson, 1991). Apart from the Euphorbiaceae, this is a different floristic composition from the one observed in parcel 2 of RNI d'Andohahela.

The gallery forest structure along the Mananara River is much like continental dry forest in Africa and the Neotropics (see Sussman & Rakotozafy, 1994 for review). Floristically, the Mananara River gallery forest is dominated by *Tamarindus in-*

dica, *Adina microcephala*, *Ficus marmorata*, and *Terminalia* sp.

The flora of parcel 2 belongs to the type Humbert and Cours Darne (1965) placed in the Southern Domain and named "Fourré à Didiereaceae et Euphorbia." The annual rainfall in this region is generally less than 500 mm and the annual average temperature is 25°C, with a large daily variation in minimum and maximum temperatures. Parcel 2 is situated in the semiarid zone (Humbert & Cours Darne, 1965). In such harsh conditions, plants exhibit many adaptations to reduce water loss, resulting in various types of convergent evolution: swollen roots and trunks (bottle trees); pachycauly; and thickened succulent, microphyllia, thorn, and deciduous leaves in dry season (Koechlin et al., 1974).

Alluaudia ascendens (Didiereaceae) is confined to the thicket and spiny vegetation that occurs in this region (Koechlin et al., 1974), and some genera such as *Adansonia* za, *Kalanchoe*, *Aloe*, *Euphorbia*, *Pachypodium*, *Ficus*, and *Uncarina* are also well represented (Koechlin et al., 1974; Ap-

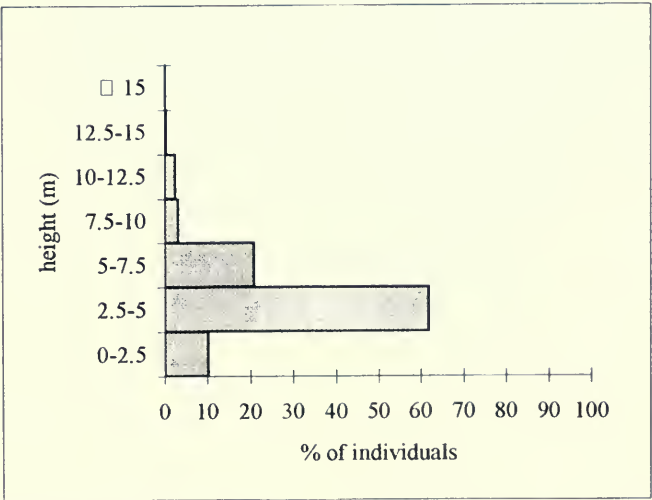


FIG. 4-7. Distribution of estimated heights in the 10 transects in parcel 2 of the RNI d'Andohahela.

pendix 4-6). Lianas belonging to families such as Apocynaceae, Asclepiadaceae, Cucurbitaceae, Passifloraceae, and Urticaceae are numerous in this forest, but they do not reach dbh measurements of ≥ 2.5 cm.

The Southern Domain is certainly less diverse climatically, topographically, and floristically than the eastern humid regions. Perrier de la Bâthie (1936) estimated that the Southern Domain contained about 336 species of plants. Even though a number of new species have been identified in this domain since his estimate (Phillipson, 1996), if we use that figure, then our 0.1 ha study site included nearly 25% of the local flora. Many plants are endemic either to the region or to Madagascar at the genus or species level. Some authors estimate that 80–85% of the flora in this region may be endemic (Koechlin et al., 1974). Didiereaceae is the only family endemic to southern Madagascar.

The main threat to the spiny forests of Madagascar is goat and cattle overgrazing, which destroys the seedlings and saplings of the larger tree species. Along the Mananara River, in the vicinity of our study site, the forest is more ruderal due to human disturbance, and the gallery forest is degraded. In the area of parcel 2 that we visited, no evidence was found for the conversion of forest into charcoal.

Both Parcels: Conclusion

The inventory methods applied to parcel 1 of RNI d'Andohahela gave a good measure of its structural and floristic composition and provided a large amount of useful data. Nevertheless, 1 ha plots are extremely time-consuming and not very practical for rapid assessment surveys. Furthermore, in topographically abrupt zones, such as that at the summit of Pic Trafonaomby, insufficient space exists for placing large plots. In contrast, the quantitative and qualitative results obtained using Gentry-style line transects in parcel 2 of the reserve indicate that this methodology is well-adapted for rapid assessment studies.

Two methodological improvements can be proposed for the type of fieldwork we conducted in the RNI d'Andohahela, particularly in humid forests: (1) use of smaller plots, combined with (2) linear surveys as proposed by Gautier et al. (1994). Linear surveys allow the quantification of plant cover and information on stratification as

well as providing valuable floristic data (Chate-lain, 1996). This method should be complemented by using small plots in order to obtain measures of basal area and biovolumes. The critical point is that standardization of rapid assessment methodologies is necessary in order to allow valid comparisons between study sites.

Our quantitative and qualitative survey of the flora in parcels 1 and 2 of the RNI d'Andohahela provides results that do not correspond completely with those expected based on the published literature. More research must be conducted to refine the effects of latitude on the structure and floristic composition of Malagasy humid forests, particularly with regard to elevational gradients. In addition to the classical floristic division into domains and elevational zones, we strongly suspect that latitudinal divisions are applicable.

Our study sites in the RNI d'Andohahela contained a rich and fascinating flora, with a high diversity of plants and types of floristic formation in a relatively small region. An extended study of the transition between the different vegetation, from the littoral forests of the eastern coast to the xerophytic thicket of the south, would allow a better understanding of the complexity of the Malagasy vegetation.

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Appendix 4-1 List of the Families Present in the Five 1 ha Permanent Plots in Parcel 1 of the RNI d’Andohahela.

	Family	Plot 1, 440 m	Plot 2, 840 m	Plot 3, 1150 m	Plot 4, 1550 m	Plot 5, 1875 m
1	Agavaceae	9.07	4.24	0.91	2.79	
2	Anacardiaceae	10.14	8.08	6.55		
3	Annonaceae	11.61	12.51	5.32		
4	Apocynaceae		1.69	2.26		
5	Aquifoliaceae	4.21	4.98	7.18	2.04	9.90
6	Araliaceae	4.25	17.94	11.47	13.59	43.24
7	Arecaceae	1.02	0.89	4.13	2.26	
8	Asteraceae				1.69	2.29
9	Bignoniaceae		6.23	0.90		
10	Burseraceae	32.97	0.83	1.10		
11	Celastraceae					10.63
12	Clusiaceae	4.42	17.88	5.01	14.67	14.10
13	Connaraceae		1.40			
14	Cunoniaceae	3.13	13.36	2.69	12.10	22.73
15	Cyatheaceae	7.66	4.47	1.85	9.29	2.52
16	Ebenaceae	19.80	7.55	4.15		
17	Elaeocarpaceae	2.76	22.01	13.67	57.68	22.34
18	Ericaceae					7.20
19	Erythroxylaceae	12.45			1.70	5.46
20	Euphorbiaceae	6.03	17.76	16.56	28.21	9.38
21	Fabaceae	7.02	4.55	0.90	3.00	
22	Flacourtiaceae	1.30	14.72	3.94	2.97	16.88
23	Hamamelidaceae			1.28	4.09	
24	Icacinales	21.77		2.05		
25	Lauraceae	9.15	17.18	38.48	35.08	47.41
26	Loganiaceae			3.38		
27	Melastomataceae		1.64			
28	Meliaceae	1.02	2.01	3.82	11.69	2.23
29	Monimiaceae	12.32	20.99	17.83	25.70	7.16
30	Moraceae	12.71	28.94	20.57	3.42	
31	Myrsinaceae	15.90	1.43	4.97	3.98	5.58
32	Myrtaceae	14.01	20.82	34.96	11.21	25.37
33	Oleaceae	1.31	4.22	3.40		
34	Pandanaceae		0.98	1.29	2.81	4.07
35	Phytenaceae	1.53				
36	Piperaceae	2.44				
37	Pittosporaceae		1.29	1.25		4.30
38	Proteaceae	2.51	3.28			
39	Rhizophoraceae				2.27	
40	Rubiaceae	35.40	18.10	18.07	13.65	18.11
41	Rutaceae		3.76	3.78	3.69	3.34
42	Sapindaceae	7.15	2.35	8.96		
43	Sapotaceae	16.55		7.72		
44	Sterculiaceae	8.37	6.54	29.05	28.53	10.79
45	Tiliaceae		1.68	2.76		
46	Verbenaceae		4.80	5.48	1.91	4.99
47	Violaceae			0.93		

Note: FIV is indicated in boldface type when the value is >10.0.

Appendix 4-2 List of the Species Present in the Five 1 ha Permanent Plots in Parcel 1 of the RNI d'Andohahela.

	Family	Genus species	Plot 1, 440 m	Plot 2, 840 m	Plot 3, 1150 m	Plot 4, 1550 m	Plot 5, 1875 m
1	Agavaceae	<i>Dracaena reflexa</i> ssp2	11.59	3.11			
2	Agavaceae	<i>Dracaena reflexa</i> ssp1	0.45	1.08	0.27	3.02	
3	Anacardiaceae	Anacardiaceae sp1		0.35			
4	Anacardiaceae	Anacardiaceae sp2			1.24		
5	Anacardiaceae	Anacardiaceae sp3		0.68	0.84		
6	Anacardiaceae	Anacardiaceae sp4		4.62	0.27		
7	Anacardiaceae	Anacardiaceae sp5		0.59			
8	Anacardiaceae	<i>Micronychia macrophylla</i>	0.45		2.35		
9	Anacardiaceae	<i>Protorhus</i> sp1		0.68			
10	Anacardiaceae	<i>Protorhus</i> sp2			0.31		
11	Anacardiaceae	<i>Sorindeia madagascariensis</i>	11.77				
12	Annonaceae	Annonaceae sp1	0.45	6.40			
13	Annonaceae	Annonaceae sp2	0.93	5.41	0.29		
14	Annonaceae	Annonaceae sp3	0.53				
15	Annonaceae	Annonaceae sp4		0.34			
16	Annonaceae	Annonaceae sp5		0.34			
17	Annonaceae	<i>Isolona</i> sp1	2.28				
18	Annonaceae	<i>Isolona</i> sp2	1.13				
19	Annonaceae	<i>Polyathia capuronii</i>	0.54				
20	Annonaceae	<i>Polyalthia</i> sp1	2.80		4.66		
21	Annonaceae	<i>Xylopia</i> sp1		0.34			
22	Annonaceae	<i>Xylopia</i> sp2			0.26		
23	Apocynaceae	Apocynaceae sp1			0.27		
24	Apocynaceae	Apocynaceae sp2			1.16		
25	Apocynaceae	<i>Cabucala</i> sp1		0.36			
26	Apocynaceae	<i>Landolphia</i> sp1		0.34			
27	Aquifoliaceae	<i>Ilex mitis</i>	15.58	6.35	8.95	0.65	10.51
28	Araliaceae	Araliaceae sp1		0.89			
29	Araliaceae	<i>Gastonia</i> sp1		0.35			
30	Araliaceae	<i>Polycias</i> sp1	5.15	8.78	5.67		
31	Araliaceae	<i>Polycias</i> sp10		1.48			
32	Araliaceae	<i>Polycias</i> sp2		1.60	1.08		
33	Araliaceae	<i>Polycias</i> sp3			0.89		
34	Araliaceae	<i>Polycias</i> sp4		0.58	0.95		
35	Araliaceae	<i>Polycias</i> sp5		0.92			
36	Araliaceae	<i>Polycias</i> sp6				1.28	
37	Araliaceae	<i>Polycias</i> sp7				0.78	32.00
38	Araliaceae	<i>Polycias</i> sp8				3.26	
39	Araliaceae	<i>Polycias</i> sp9				7.16	11.77
40	Araliaceae	<i>Schefflera</i> sp1		1.61	1.23		
41	Araliaceae	<i>Schefflera</i> sp2					2.60
42	Araliaceae	<i>Schefflera</i> sp3		1.38			
43	Araliaceae	<i>Schefflera</i> sp4			0.85		
44	Arecaceae	<i>Dypsis</i> spp	4.94	0.39	4.99	1.61	
45	Asteraceae	<i>Brachylaena ramiflora</i>					0.72
46	Asteraceae	<i>Vernonia</i> sp1				0.46	
47	Bignoniaceae	<i>Colea</i> sp1			0.26		
48	Bignoniaceae	<i>Ophiocolea floribunda</i>		6.87			
49	Bignoniaceae	<i>Rohdocolea linearis</i>		0.42			
50	Burseraceae	<i>Canarium boivinii</i>	0.45		0.61		
51	Burseraceae	<i>Canarium</i> sp1		0.34			
52	Celastraceae	<i>Brexiella</i> sp1					11.68
53	Clusiaceae	Clusiaceae sp1	2.41	0.43			
54	Clusiaceae	Clusiaceae sp2	1.63	3.66			
55	Clusiaceae	Clusiaceae sp3	2.36	0.46			
56	Clusiaceae	Clusiaceae sp4	0.53	1.54			
57	Clusiaceae	<i>Garcinia</i> sp1	0.48	1.05			
58	Clusiaceae	<i>Garcinia</i> sp2	0.90	0.37			16.45
59	Clusiaceae	<i>Harungana</i> sp1		0.67			

Appendix 4-2 Continued.

	Family	Genus species	Plot 1, 440 m	Plot 2, 840 m	Plot 3, 1150 m	Plot 4, 1550 m	Plot 5, 1875 m
60	Clusiaceae	<i>Mammea</i> sp1		0.70	5.13	4.79	
61	Clusiaceae	<i>Mammea</i> sp2	1.24			0.60	
62	Clusiaceae	<i>Mammea</i> sp3	19.67	3.31			
63	Clusiaceae	<i>Ochrocarpus</i> sp1	1.87	1.06		2.26	
64	Clusiaceae	<i>Ochrocarpus</i> sp2	1.70	2.64			
65	Clusiaceae	<i>Ochrocarpus</i> sp3		0.40			
66	Clusiaceae	<i>Ochrocarpus</i> sp4			0.26	3.73	
67	Clusiaceae	<i>Symphonia</i> sp1				2.11	
68	Connaraceae	<i>Ellipanthus</i> sp1			1.06		
69	Cunoniaceae	<i>Weinmannia</i> sp1	1.37	2.27			
70	Cunoniaceae	<i>Weinmannia</i> sp2	0.70	1.54			
71	Cunoniaceae	<i>Weinmannia</i> sp3	0.87	4.36			
72	Cunoniaceae	<i>Weinmannia</i> sp4			0.84	15.54	12.20
73	Cunoniaceae	<i>Weinmannia</i> sp5		5.56			
74	Cunoniaceae	<i>Weinmannia</i> sp6			1.33		6.82
75	Cunoniaceae	<i>Weinmannia</i> sp7					2.92
76	Cyatheaceae	<i>Cyathea</i> sp1	3.56	4.62	2.42	12.42	1.39
77	Cyatheaceae	<i>Cyathea</i> sp2		0.35			
78	Ebenaceae	<i>Diospyros</i> sp1	0.46	0.85	1.05		
79	Ebenaceae	<i>Diospyros</i> sp2	0.96	0.71	1.81		
80	Ebenaceae	<i>Diospyros</i> sp3	3.76	5.55			
81	Ebenaceae	<i>Diospyros</i> sp4	0.98	0.50			
82	Ebenaceae	<i>Diospyros</i> sp5	0.91				
83	Ebenaceae	<i>Diospyros</i> sp6			0.59		
84	Elaeocarpaceae	<i>Elaeocarpus</i> sp1		1.12			
85	Elaeocarpaceae	<i>Elaeocarpus</i> sp2			0.93		
86	Elaeocarpaceae	<i>Elaeocarpus</i> sp3				0.52	
87	Elaeocarpaceae	<i>Elaeocarpus</i> sp4					5.95
88	Elaeocarpaceae	<i>Elaeocarpus</i> sp5			3.96		
89	Elaeocarpaceae	<i>Elaeocarpus</i> sp6		0.35			
90	Elaeocarpaceae	<i>Sloanea rhodantha</i>	3.74	22.60	11.83	57.93	18.65
91	Ericaceae	<i>Agauria</i> sp1					7.37
92	Erythroxylaceae	<i>Erythroxylum</i> sp1	16.93				
93	Erythroxylaceae	<i>Erythroxylum</i> sp2	0.96				
94	Erythroxylaceae	<i>Erythroxylum</i> sp3				0.47	
95	Erythroxylaceae	<i>Erythroxylum</i> sp4					6.50
96	Euphorbiaceae	<i>Antidesma petiolare</i>	1.16		0.81		
97	Euphorbiaceae	<i>Antidesma</i> sp1			1.32		
98	Euphorbiaceae	<i>Bridelia pervilleana</i>	2.81	1.10			
99	Euphorbiaceae	<i>Bridelia tulasneana</i>		2.00			
100	Euphorbiaceae	<i>Croton monge</i>	0.76	1.95	3.27		
101	Euphorbiaceae	<i>Croton</i> sp1			1.97	3.72	
102	Euphorbiaceae	<i>Croton</i> sp2				0.49	0.66
103	Euphorbiaceae	<i>Croton</i> sp3					2.60
104	Euphorbiaceae	<i>Croton</i> sp4	1.32				
105	Euphorbiaceae	<i>Croton</i> sp5			0.27		
106	Euphorbiaceae	<i>Dryptetes madagascariensis</i>		2.79	0.53		
107	Euphorbiaceae	<i>Drypetes</i> sp1			0.26	0.53	
108	Euphorbiaceae	<i>Drypetes</i> sp2		0.35			
109	Euphorbiaceae	<i>Drypetes</i> sp3			0.53		
110	Euphorbiaceae	Euphorbiaceae sp1		0.34			
111	Euphorbiaceae	Euphorbiaceae sp2			1.90		
112	Euphorbiaceae	<i>Macaranga cuspidata</i>	0.54				
113	Euphorbiaceae	<i>Macaranga</i> sp1		7.41	0.91		
114	Euphorbiaceae	<i>Macaranga</i> sp2		0.82	0.83	27.30	3.59
115	Euphorbiaceae	<i>Macaranga</i> sp3		1.23			
116	Euphorbiaceae	<i>Phyllanthus</i> sp1			0.98		
117	Euphorbiaceae	<i>Phyllanthus</i> sp2			0.27		
118	Euphorbiaceae	<i>Suregada</i> sp1	2.15				
119	Euphorbiaceae	<i>Uapaca</i> sp1	1.43				

Appendix 4-2 *Continued.*

	Family	Genus species	Plot 1, 440 m	Plot 2, 840 m	Plot 3, 1150 m	Plot 4, 1550 m	Plot 5, 1875 m
120	Fabaceae	<i>Albizzia gumifera</i>		1.12			
121	Fabaceae	<i>Albizzia</i> sp1	1.69				
122	Fabaceae	Fabaceae sp1	4.74	3.92			
123	Fabaceae	Fabaceae sp2	0.55				
124	Fabaceae	Fabaceae sp3			0.26		
125	Fabaceae	<i>Strongylodon</i> sp1				3.52	
126	Flacourtiaceae	<i>Aphloia theaeformis</i>	0.54		0.26	2.62	14.67
127	Flacourtiaceae	<i>Casearia</i> sp1	1.09	2.47			
128	Flacourtiaceae	Flacourtiaceae sp1	2.15	6.01			4.30
129	Flacourtiaceae	Flacourtiaceae sp2	0.92	1.10			
130	Flacourtiaceae	Flacourtiaceae sp3	0.55				
131	Flacourtiaceae	<i>Scolopia</i> sp1		4.25	1.05		
132	Flacourtiaceae	<i>Tisonia</i> sp1	0.45	3.08	0.26		
133	Flacourtiaceae	<i>Tisonia</i> sp2			0.27		
134	Hamamelidaceae	<i>Dicoryphe</i> sp1			1.10	4.32	
135	Icacinaceae	<i>Desmatostachys</i> sp1	0.98				
136	Icacinaceae	Icacinaceae sp1			1.57		
137	Lauraceae	<i>Belschmedia</i> sp1					14.97
138	Lauraceae	<i>Cinnamosma</i> sp1	0.54				
139	Lauraceae	<i>Cryptocarya</i> sp1		2.39	4.41		
140	Lauraceae	<i>Cryptocarya</i> sp2		1.61			
141	Lauraceae	<i>Cryptocarya</i> sp3		0.34			10.28
142	Lauraceae	<i>Cryptocarya</i> sp4		0.37			
143	Lauraceae	Lauraceae sp1	0.92		1.58	1.01	2.86
144	Lauraceae	Lauraceae sp10			12.13	20.73	
145	Lauraceae	Lauraceae sp11				1.07	
146	Lauraceae	Lauraceae sp12			5.94		
147	Lauraceae	Lauraceae sp13			5.51		
148	Lauraceae	Lauraceae sp14			6.62		
149	Lauraceae	Lauraceae sp15				9.49	
150	Lauraceae	Lauraceae sp16					2.19
151	Lauraceae	Lauraceae sp2	1.74	0.37			
152	Lauraceae	Lauraceae sp3	11.47				4.40
153	Lauraceae	Lauraceae sp4	1.75			1.20	
154	Lauraceae	Lauraceae sp5	0.45	0.72			
155	Lauraceae	Lauraceae sp6	0.86				8.73
156	Lauraceae	Lauraceae sp7			0.63		
157	Lauraceae	Lauraceae sp8		1.05	5.76	0.52	
158	Lauraceae	Lauraceae sp9			1.12		
159	Lauraceae	<i>Ocotea</i> sp1	0.45	8.42	0.28		
160	Lauraceae	<i>Ocotea</i> sp2		1.00			
161	Lauraceae	<i>Ocotea</i> sp3	1.08				4.76
162	Lauraceae	<i>Ocotea</i> sp4	0.79				
163	Lauraceae	<i>Ocotea trichophebia</i>	0.45				
164	Lauraceae	<i>Potameia</i> sp1				3.56	
165	Loganiaceae	<i>Anthocleista madagascariensis</i>			2.88		
166	Loganiaceae	Loganiaceae sp1			0.28		
167	Melastomataceae	<i>Memecylon</i> sp1		1.34	2.63		
168	Meliaceae	<i>Malleastrum gracile</i>		1.06	1.27	0.95	
169	Meliaceae	<i>Malleastrum</i> sp1				12.37	0.66
170	Meliaceae	<i>Malleastrum</i> sp2		0.34			
171	Meliaceae	<i>Malleastrum</i> sp3			0.26		
172	Meliaceae	<i>Turraea</i> sp1	0.45				
173	Monimiaceae	<i>Decarydendron</i> sp1		0.35			
174	Monimiaceae	<i>Ephippiandra</i> sp1					8.20
175	Monimiaceae	Monimiaceae sp1				18.76	
176	Monimiaceae	Monimiaceae sp2		0.34	2.07	2.47	
177	Monimiaceae	Monimiaceae sp3		0.34		0.94	
178	Monimiaceae	<i>Tambourissa</i> sp1	1.25	7.00		6.44	
179	Monimiaceae	<i>Tambourissa</i> sp2	12.43	6.80	8.65		

Appendix 4-2 Continued.

	Family	Genus species	Plot 1, 440 m	Plot 2, 840 m	Plot 3, 1150 m	Plot 4, 1550 m	Plot 5, 1875 m
180	Monimiaceae	<i>Tambourissa</i> sp3	0.46	2.69			
181	Monimiaceae	<i>Tambourissa</i> sp4		1.86	8.96		
182	Monimiaceae	<i>Tambourissa</i> sp5		3.18			
183	Monimiaceae	<i>Tambourissa</i> sp6		1.05			
184	Monimiaceae	<i>Tambourissa</i> sp7			0.44		
185	Moraceae	<i>Streblus</i> sp1		1.80			
186	Moraceae	<i>Ficus sorocoides</i>		0.34		0.49	
187	Moraceae	<i>Ficus</i> sp1			3.28		
188	Moraceae	<i>Ficus</i> sp2		0.71	0.27	0.47	
189	Moraceae	<i>Ficus</i> sp3			1.81		
190	Moraceae	<i>Ficus</i> sp4			1.26		
191	Moraceae	Moraceae sp1	7.13	7.47			
192	Moraceae	Moraceae sp2	0.46	2.36	13.15		
193	Moraceae	Moraceae sp3	0.52	0.35			
194	Moraceae	Moraceae sp4	0.45	0.68			
195	Moraceae	Moraceae sp5	0.50				
196	Moraceae	Moraceae sp6		0.35			
197	Moraceae	Moraceae sp7		0.83			
198	Moraceae	Moraceae sp8		0.70			
199	Moraceae	Moraceae sp9		0.38			
200	Moraceae	<i>Streblus</i> sp2		0.36			
201	Moraceae	<i>Streblus dinepate</i>	0.53	7.53			
202	Moraceae	<i>Streblus mauritianus</i>		2.02			
203	Moraceae	<i>Treculia</i> sp1	2.14				
204	Moraceae	<i>Trilepisium madagascariensis</i>		2.07	1.77		
205	Moraceae	<i>Trophis montana</i>		0.35			
206	Myrsinaceae	<i>Oncostemum</i> sp11				0.49	
207	Myrsinaceae	<i>Oncostemum</i> sp1	0.54				
208	Myrsinaceae	<i>Oncostemum</i> sp10		1.31			
209	Myrsinaceae	<i>Oncostemum</i> sp12					6.19
210	Myrsinaceae	<i>Oncostemum</i> sp2	8.33				
211	Myrsinaceae	<i>Oncostemum</i> sp3	1.10		1.17		
212	Myrsinaceae	<i>Oncostemum</i> sp4	1.34		0.54		
213	Myrsinaceae	<i>Oncostemum</i> sp5	0.45				
214	Myrsinaceae	<i>Oncostemum</i> sp6	1.15				
215	Myrsinaceae	<i>Oncostemum</i> sp7	0.45				
216	Myrsinaceae	<i>Oncostemum</i> sp8	0.45			1.92	
217	Myrsinaceae	<i>Oncostemum</i> sp9	0.46				
218	Myrtaceae	<i>Eugenia emirnense</i>	2.13				
219	Myrtaceae	Myrtaceae sp1	0.59	5.72			
220	Myrtaceae	Myrtaceae sp10		0.34			
221	Myrtaceae	Myrtaceae sp11		8.47			
222	Myrtaceae	Myrtaceae sp12			2.78		
223	Myrtaceae	Myrtaceae sp13			13.64		
224	Myrtaceae	Myrtaceae sp14			0.27		
225	Myrtaceae	Myrtaceae sp15				6.61	
226	Myrtaceae	Myrtaceae sp16				3.85	
227	Myrtaceae	Myrtaceae sp17					1.18
228	Myrtaceae	Myrtaceae sp18					2.23
229	Myrtaceae	Myrtaceae sp19					0.68
230	Myrtaceae	Myrtaceae sp2		1.26			
231	Myrtaceae	Myrtaceae sp20					6.31
232	Myrtaceae	Myrtaceae sp21					1.32
233	Myrtaceae	Myrtaceae sp22					4.86
234	Myrtaceae	Myrtaceae sp3	0.59	0.72		0.57	
235	Myrtaceae	Myrtaceae sp4	1.07		3.38		
236	Myrtaceae	Myrtaceae sp5		0.35	17.00		
237	Myrtaceae	Myrtaceae sp6			0.39		
238	Myrtaceae	Myrtaceae sp7	7.39				
239	Myrtaceae	Myrtaceae sp8		0.38	2.36		

Appendix 4-2 Continued.

	Family	Genus species	Plot 1, 440 m	Plot 2, 840 m	Plot 3, 1150 m	Plot 4, 1550 m	Plot 5, 1875 m
240	Myrtaceae	Myrtaceae sp9		5.58			
241	Myrtaceae	<i>Syzygium</i> sp1	2.10				
242	Myrtaceae	<i>Syzygium</i> sp2					5.65
243	Oleaceae	<i>Noronhia</i> sp1	0.99		0.58		
244	Oleaceae	<i>Noronhia</i> sp2		4.32			
245	Oleaceae	<i>Noronhia</i> sp3		0.41			
246	Oleaceae	<i>Noronhia</i> sp4			0.30		
247	Oleaceae	<i>Noronhia</i> sp5			1.06		
248	Pandanaceae	<i>Pandanus</i> sp1				2.75	
249	Pandanaceae	<i>Pandanus</i> sp2			1.10		4.68
250	Pandanaceae	<i>Pandanus</i> sp3		0.67			
251	Phytenaceae	<i>Phytena madagascariensis</i>	1.21				
252	Piperaceae	<i>Piper</i> sp1	1.29				
253	Pittosporaceae	<i>Pittosporum</i> sp1		0.99	0.91		4.90
254	Proteaceae	<i>Dilobeia thouarsii</i>	2.69	3.72			
255	Rhizophoraceae	Rhizophoraceae sp1				1.04	
256	Rubiaceae	<i>Breonia</i> sp1		3.23			
257	Rubiaceae	<i>Craterispermum</i> sp1		0.37			
258	Rubiaceae	<i>Gaertnera</i> sp1	3.01				
259	Rubiaceae	<i>Gaertnera</i> sp2	0.96	1.08			
260	Rubiaceae	<i>Gaertnera</i> sp3			1.81		
261	Rubiaceae	<i>Gaertnera</i> sp4			5.05		
262	Rubiaceae	<i>Gaertnera</i> sp5					0.96
263	Rubiaceae	<i>Hyperacanthus</i> sp1	11.36				
264	Rubiaceae	<i>Hyperacanthus</i> sp2	4.98				
265	Rubiaceae	<i>Ixora</i> sp1				1.06	
266	Rubiaceae	<i>Pouridiantha</i> sp1				0.47	
267	Rubiaceae	<i>Psychotria</i> sp1	0.51	1.17	0.27		
268	Rubiaceae	<i>Psychotria</i> sp2		0.68			
269	Rubiaceae	<i>Psychotria</i> sp3			0.56		
270	Rubiaceae	<i>Psychotria</i> sp4			0.53		
271	Rubiaceae	<i>Psychotria</i> sp5			0.32		
272	Rubiaceae	<i>Psychotria</i> sp6				0.93	
273	Rubiaceae	<i>Psychotria</i> sp7					0.67
274	Rubiaceae	<i>Rothmania</i> sp1			0.30		
275	Rubiaceae	Rubiaceae sp1	1.23	4.73			6.39
276	Rubiaceae	Rubiaceae sp10			0.52		
277	Rubiaceae	Rubiaceae sp11		1.05			
278	Rubiaceae	Rubiaceae sp12			0.53		
279	Rubiaceae	Rubiaceae sp13			0.83		
280	Rubiaceae	Rubiaceae sp14				0.49	
281	Rubiaceae	Rubiaceae sp15				2.41	
282	Rubiaceae	Rubiaceae sp16				0.94	
283	Rubiaceae	Rubiaceae sp17					5.02
284	Rubiaceae	Rubiaceae sp18					3.77
285	Rubiaceae	Rubiaceae sp2	4.77	1.33	0.78		
286	Rubiaceae	Rubiaceae sp3	0.61		1.58		
287	Rubiaceae	Rubiaceae sp4	0.55				
288	Rubiaceae	Rubiaceae sp5	0.94	1.04			
289	Rubiaceae	Rubiaceae sp6	4.04	0.75			
290	Rubiaceae	Rubiaceae sp7	0.55	1.34			
291	Rubiaceae	Rubiaceae sp8	0.59				
292	Rubiaceae	Rubiaceae sp9	0.47		0.62		
293	Rubiaceae	<i>Schysmatoclada</i> sp1				1.40	
294	Rubiaceae	<i>Tarenna</i> sp1	1.31				
295	Rutaceae	<i>Vepris</i> sp1					2.21
296	Rutaceae	<i>Vepris</i> sp2				0.94	
297	Rutaceae	<i>Vepris</i> sp3			0.27		
298	Rutaceae	<i>Vepris</i> sp4		1.41	0.29		
299	Rutaceae	<i>Vepris</i> sp5			0.27		

Appendix 4-2 Continued.

	Family	Genus species	Plot 1, 440 m	Plot 2, 840 m	Plot 3, 1150 m	Plot 4, 1550 m	Plot 5, 1875 m
300	Rutaceae	<i>Zanthoxylum</i> sp1		2.67	0.56	0.59	
301	Sapindaceae	<i>Allophylus cobbe</i>	1.46				
302	Sapindaceae	<i>Allophylus</i> sp1		0.84			
303	Sapindaceae	<i>Allophylus</i> sp2			8.45		
304	Sapindaceae	<i>Macphersonia</i> sp1			0.54		
305	Sapindaceae	<i>Plagioscyphus</i> sp1	1.06				
306	Sapindaceae	<i>Plagioscyphus</i> sp2	3.92				
307	Sapindaceae	Sapindaceae sp1		0.89	1.66		
308	Sapotaceae	<i>Capurodendron</i> sp1	0.58				
309	Sapotaceae	<i>Chrysophyllum boivinianum</i>	17.85		6.87		
310	Sapotaceae	<i>Mimusops</i> sp1			0.29		
311	Sapotaceae	Sapotaceae sp1			0.31		
312	Sterculiaceae	<i>Dombeya</i> sp1	0.49	0.70		4.83	
313	Sterculiaceae	<i>Dombeya</i> sp10				2.72	
314	Sterculiaceae	<i>Dombeya</i> sp11				3.33	
315	Sterculiaceae	<i>Dombeya</i> sp12					2.21
316	Sterculiaceae	<i>Dombeya</i> sp2	3.67	0.71		9.42	1.50
317	Sterculiaceae	<i>Dombeya</i> sp3	1.21	0.42	9.60		
318	Sterculiaceae	<i>Dombeya</i> sp4	0.47	1.82			
319	Sterculiaceae	<i>Dombeya</i> sp5	1.18	1.17		4.66	
320	Sterculiaceae	<i>Dombeya</i> sp6			0.83		
321	Sterculiaceae	<i>Dombeya</i> sp7			2.61		
322	Sterculiaceae	<i>Dombeya</i> sp8				0.97	
323	Sterculiaceae	<i>Dombeya</i> sp9			18.38	5.37	
324	Sterculiaceae	Sterculiaceae sp1			0.90		
325	Sterculiaceae	Sterculiaceae sp2					3.68
326	Tiliaceae	<i>Grewia</i> sp1		0.34	3.77		
327	Tiliaceae	<i>Grewia</i> sp2		0.35			
328	Verbenaceae	<i>Clerodendrum</i> sp1		1.01	0.26	0.69	
329	Verbenaceae	<i>Vitex</i> sp1		0.38	1.92		
330	Verbenaceae	<i>Vitex</i> sp2			0.27		
331	Verbenaceae	<i>Vitex</i> sp3		0.90			
332	Verbenaceae	<i>Vitex</i> sp4					5.16
333	Verbenaceae	<i>Vitex</i> sp5		1.28			
334	Verbenaceae	<i>Vitex</i> sp6			2.29		
335	Violaceae	<i>Rinorea</i> sp1			0.29		

Note: IVI is indicated in boldface type when the value is >10.0.

Appendix 4-3 Relative Density, Relative Dominance, Relative Specific Diversity, and FIV.

Plot 1 at 440 m

Family	Number of individuals	Relative density (%)	Basal area (cm ²)	Relative dominance (%)	Number of species	Relative specific diversity (%)	FIV
Rubiaceae	79	13.23	27,338.78	9.77	15	12.40	35.40
Clusiaceae	62	10.39	40,056.69	14.32	10	8.26	32.97
Lauraceae	41	6.87	16,267.57	5.81	11	9.09	21.77
Elaeocarpaceae	18	3.02	42,346.69	15.13	2	1.65	19.80
Sapotaceae	29	4.86	28,087.17	10.04	2	1.65	16.55
Myrsinaceae	39	6.53	5,409.25	1.93	9	7.44	15.90
Myrtaceae	26	4.36	13,153.73	4.70	6	4.96	14.01
Moraceae	22	3.69	9,077.59	3.24	7	5.79	12.71
Euphorbiaceae	19	3.18	9,740.10	3.48	7	5.79	12.45
Monimiaceae	34	5.70	11,586.79	4.14	3	2.48	12.32
Aquifoliaceae	31	5.19	15,641.56	5.59	1	0.83	11.61
Annonaceae	19	3.18	3,287.83	1.18	7	5.79	10.14
Liliaceae	30	5.03	6,910.59	2.47	2	1.65	9.15
Anacardiaceae	34	5.70	4,822.35	1.72	2	1.65	9.07
Sterculiaceae	14	2.35	5,303.65	1.90	5	4.13	8.37
Ebenaceae	15	2.51	2,848.21	1.02	5	4.13	7.66
Sapindaceae	8	1.34	9,330.39	3.33	3	2.48	7.15
Flacourtiaceae	11	1.84	2,911.73	1.04	5	4.13	7.02
Fabaceae	11	1.84	4,788.25	1.71	3	2.48	6.03
Cunoniaceae	8	1.34	1,673.17	0.60	3	2.48	4.42
Arecaceae	7	1.17	6,294.33	2.25	1	0.83	4.25
Araliaceae	9	1.51	5,257.12	1.88	1	0.83	4.21
Cyatheaceae	11	1.84	1,283.29	0.46	1	0.83	3.13
Erythroxylaceae	5	0.84	752.33	0.27	2	1.65	2.76
Proteaceae	4	0.67	2,829.77	1.01	1	0.83	2.51
Piperaceae	3	0.50	788.06	0.28	2	1.65	2.44
Physenaceae	2	0.34	1,040.20	0.37	1	0.83	1.53
Oleaceae	2	0.34	417.40	0.15	1	0.83	1.31
Icacinaceae	2	0.34	395.87	0.14	1	0.83	1.30
Burseraceae	1	0.17	80.12	0.03	1	0.83	1.02
Meliaceae	1	0.17	80.12	0.03	1	0.83	1.02
Total	597	100.0	279,800.69	100.00	121	100.00	300.00

Plot 2 at 840 m

Family	Number of individuals	Relative density (%)	Basal area (cm ²)	Relative dominance (%)	Number of species	Relative specific diversity (%)	FIV
Moraceae	71	9.13	34,574.26	8.93	16	10.88	28.94
Elaeocarpaceae	44	5.66	55,429.15	14.31	3	2.04	22.01
Monimiaceae	72	9.25	21,729.45	5.61	9	6.12	20.99
Myrtaceae	60	7.71	29,691.56	7.66	8	5.44	20.82
Rubiaceae	45	5.78	18,726.10	4.83	11	7.48	18.10
Araliaceae	51	6.56	20,402.74	5.27	9	6.12	17.94
Clusiaceae	45	5.78	12,596.73	3.25	13	8.84	17.88
Euphorbiaceae	55	7.07	17,680.37	4.56	9	6.12	17.76
Lauraceae	36	4.63	24,920.31	6.43	9	6.12	17.18
Flacourtiaceae	43	5.53	22,435.90	5.79	5	3.40	14.72
Cunoniaceae	47	6.04	18,942.32	4.89	4	2.72	13.65
Annonaceae	26	3.34	22,343.31	5.77	5	3.40	12.51
Anacardiaceae	16	2.06	10,168.99	2.63	5	3.40	8.08
Ebenaceae	17	2.19	10,231.58	2.64	4	2.72	7.55
Sterculiaceae	9	1.16	7,681.01	1.98	5	3.40	6.54
Bignoniaceae	21	2.70	8,393.33	2.17	2	1.36	6.23
Aquifoliaceae	18	2.31	7,711.92	1.99	1	0.68	4.98

Appendix 4-3 *Continued.*

Family	Number of individu- als	Relative density (%)	Basal area (cm²)	Relative dominance (%)	Number of species	Relative specific diversity (%)	FIV
Verbenaceae	9	1.16	3,571.53	0.92	4	2.72	4.80
Fabaceae	15	1.93	4,871.78	1.26	2	1.36	4.55
Cyatheaceae	15	1.93	4,572.73	1.18	2	1.36	4.47
Agavaceae	9	1.16	6,664.90	1.72	2	1.36	4.24
Oleaceae	14	1.80	4,109.24	1.06	2	1.36	4.22
Rutaceae	10	1.29	4,330.37	1.12	2	1.36	3.76
Proteaceae	6	0.77	7,079.89	1.83	1	0.68	3.28
Sapindaceae	4	0.51	1,851.72	0.48	2	1.36	2.35
Meliaceae	4	0.51	527.36	0.14	2	1.36	2.01
Apocynaceae	2	0.26	289.65	0.07	2	1.36	1.69
Tiliaceae	2	0.26	249.95	0.06	2	1.36	1.68
Melastomataceae	3	0.39	2,241.13	0.58	1	0.68	1.64
Myrsinaceae	3	0.39	1,398.92	0.36	1	0.68	1.43
Pittosporaceae	2	0.26	1,383.79	0.36	1	0.68	1.29
Pandanaceae	2	0.26	165.13	0.04	1	0.68	0.98
Arecaceae	1	0.13	298.65	0.08	1	0.68	0.89
Burseraceae	1	0.13	100.29	0.03	1	0.68	0.83
Total	778	100.00	387,366.02	100.00	147	100.00	300.00

Plot 3 at 1150 m

Family	Number of individuals	Relative density (%)	Basal area (cm²)	Relative dominance (%)	Number of species	Relative specific diversity (%)	FIV
Lauraceae	156	13.82	73,299.19	16.78	10	7.87	38.48
Myrtaceae	183	16.21	57,833.38	13.24	7	5.51	34.96
Sterculiaceae	95	8.41	72,905.35	16.69	5	3.94	29.05
Moraceae	88	7.79	35,171.15	8.05	6	4.72	20.57
Rubiaceae	64	5.67	9,462.54	2.17	13	10.24	18.07
Monimiaceae	73	6.47	35,854.02	8.21	4	3.15	17.83
Euphorbiaceae	47	4.16	9,440.24	2.16	13	10.24	16.56
Elaeocarpaceae	58	5.14	26,951.31	6.17	3	2.36	13.67
Araliaceae	38	3.37	14,753.81	3.38	6	4.72	11.47
Sapindaceae	41	3.63	12,950.96	2.97	3	2.36	8.96
Sapotaceae	23	2.04	14,501.25	3.32	3	2.36	7.72
Aquifoliaceae	29	2.57	16,693.73	3.82	1	0.79	7.18
Anacardiaceae	19	1.68	4,043.29	0.93	5	3.94	6.55
Verbenaceae	18	1.59	3,212.26	0.74	4	3.15	5.48
Annonaceae	21	1.86	4,805.67	1.10	3	2.36	5.32
Clusiaceae	22	1.95	6,493.99	1.49	2	1.57	5.01
Myrsinaceae	12	1.06	3,311.80	0.76	4	3.15	4.97
Ebenaceae	13	1.15	2,774.52	0.64	3	2.36	4.15
Arecaceae	19	1.68	7,237.66	1.66	1	0.79	4.13
Flacourtiaceae	7	0.62	732.78	0.17	4	3.15	3.94
Meliaceae	18	1.59	2,851.39	0.65	2	1.57	3.82
Rutaceae	5	0.44	832.05	0.19	4	3.15	3.78
Oleaceae	7	0.62	1,811.98	0.41	3	2.36	3.40
Loganiaceae	12	1.06	3,233.12	0.74	2	1.57	3.38
Tiliaceae	14	1.24	3,189.71	0.73	1	0.79	2.76
Cunoniaceae	8	0.71	1,793.82	0.41	2	1.57	2.69
Apocynaceae	5	0.44	1,042.20	0.24	2	1.57	2.26
Icacinaceae	4	0.35	3,981.43	0.91	1	0.79	2.05
Cyatheaceae	9	0.80	1,161.74	0.27	1	0.79	1.85
Connaraceae	3	0.27	1,517.17	0.35	1	0.79	1.40
Pandanaceae	4	0.35	649.50	0.15	1	0.79	1.29
Hamamelidaceae	4	0.35	615.10	0.14	1	0.79	1.28

Appendix 4-3 *Continued.*

Family	Number of individuals	Relative density (%)	Basal area (cm ²)	Relative dominance (%)	Number of species	Relative specific diversity (%)	FIV
Pittosporaceae	4	0.35	460.33	0.11	1	0.79	1.25
Burseraceae	2	0.18	580.69	0.13	1	0.79	1.10
Violaceae	1	0.09	226.98	0.05	1	0.79	0.93
Agavaceae	1	0.09	143.14	0.03	1	0.79	0.91
Fabaceae	1	0.09	93.31	0.02	1	0.79	0.90
Bignoniaceae	1	0.09	91.61	0.02	1	0.79	0.90
Total	1,129	100.00	436,704.17	100.00	127	100.00	300.00

Plot 4 at 1550 m

Family	Number of individuals	Relative density (%)	Basal area (cm ²)	Relative dominance (%)	Number of species	Relative specific diversity (%)	FIV
Elaeocarpaceae	26	4.17	297,370.02	48.96	3	4.55	57.68
Lauraceae	94	15.09	56,990.94	9.38	7	10.61	35.08
Sterculiaceae	74	11.88	36,701.04	6.04	7	10.61	28.53
Euphorbiaceae	106	17.01	31,169.85	5.13	4	6.06	28.21
Monimiaceae	54	8.67	57,441.91	9.46	5	7.58	25.70
Clusiaceae	32	5.14	11,870.89	1.95	5	7.58	14.67
Rubiaceae	16	2.57	2,908.71	0.48	7	10.61	13.65
Araliaceae	31	4.98	15,531.19	2.56	4	6.06	13.59
Cunoniaceae	42	6.74	23,366.95	3.85	1	1.52	12.10
Meliaceae	29	4.65	24,333.28	4.01	2	3.03	11.69
Myrtaceae	20	3.21	20,956.63	3.45	3	4.55	11.21
Cyatheaceae	41	6.58	7,224.38	1.19	1	1.52	9.29
Hamamelidaceae	9	1.44	6,853.60	1.13	1	1.52	4.09
Myrsinaceae	5	0.80	891.02	0.15	2	3.03	3.98
Rutaceae	3	0.48	1,058.80	0.17	2	3.03	3.69
Moraceae	2	0.32	397.00	0.07	2	3.03	3.42
Fabaceae	8	1.28	1,230.35	0.20	1	1.52	3.00
Flacourtiaceae	7	1.12	2,004.74	0.33	1	1.52	2.97
Pandanaceae	7	1.12	1,062.36	0.17	1	1.52	2.81
Agavaceae	7	1.12	909.27	0.15	1	1.52	2.79
Rhizophoraceae	1	0.16	3,599.71	0.59	1	1.52	2.27
Arecaceae	3	0.48	1,570.40	0.26	1	1.52	2.26
Aquifoliaceae	2	0.32	1,210.34	0.20	1	1.52	2.04
Verbenaceae	2	0.32	467.98	0.08	1	1.52	1.91
Erythroxylaceae	1	0.16	143.14	0.02	1	1.52	1.70
Asteraceae	1	0.16	83.32	0.01	1	1.52	1.69
Total	623	100.00	607,347.82	100.00	66	100.00	300.00

Plot 5 at 1875 m

Family	Number of individuals	Relative density (%)	Basal area (cm ²)	Relative dominance (%)	Number of species	Relative specific diversity (%)	FIV
Lauraceae	183	13.62	128,961.25	19.79	7	14.00	47.41
Araliaceae	233	17.35	129,617.75	19.89	3	6.00	43.24
Myrtaceae	105	7.84	23,037.00	3.54	7	14.00	25.37
Cunoniaceae	70	5.22	74,959.50	11.50	3	6.00	22.73
Elaeocarpaceae	75	5.60	70,012.50	10.74	3	6.00	22.34
Rubiaceae	73	5.41	17,598.25	2.70	5	10.00	18.11
Flacourtiaceae	83	6.16	43,814.50	6.72	2	4.00	16.88
Clusiaceae	105	7.84	27,789.75	4.26	1	2.00	14.10

Appendix 4-3 *Continued.*

Family	Number of individuals	Relative density (%)	Basal area (cm²)	Relative dominance (%)	Number of species	Relative specific diversity (%)	FIV
Sterculiaceae	33	2.43	15,380.25	2.36	3	6.00	10.79
Celastraceae	75	5.60	19,788.25	3.04	1	2.00	10.63
Aquifoliaceae	53	3.92	25,937.75	3.98	1	2.00	9.90
Euphorbiaceae	30	2.24	7,427.00	1.14	3	6.00	9.38
Ericaceae	18	1.31	25,367.75	3.89	1	2.00	7.20
Monimiaceae	45	3.36	11,739.00	1.80	1	2.00	7.16
Myrsinaceae	38	2.80	5,109.50	0.78	1	2.00	5.58
Erythroxylaceae	35	2.61	5,508.25	0.85	1	2.00	5.46
Verbenaceae	30	2.24	4,880.75	0.75	1	2.00	4.99
Pittosporaceae	18	1.31	6,451.50	0.99	1	2.00	4.30
Pandanaceae	20	1.49	3,772.00	0.58	1	2.00	4.07
Rutaceae	13	0.93	2,631.50	0.40	1	2.00	3.34
Cyatheaceae	5	0.37	956.75	0.15	1	2.00	2.52
Asteraceae	3	0.19	672.00	0.10	1	2.00	2.29
Meliaceae	3	0.19	259.75	0.04	1	2.00	2.23
Total	1,340	100.00	651,672.50	100.00	50	100.00	300.00

Note: Data are organized by decreasing values for each plot, and the unidentified material is omitted.

Appendix 4-4 Relative Density, Relative Dominance, Relative Frequency, and IVI.

Plot 1 at 440 m

Family	Genus species	Number of individuals	Relative density (%)	Basal area (cm ²)	Relative dominance (%)	Absolute frequency	Relative frequency	IVI
Clusiaceae	<i>Mammea</i> sp3	38	6.37	26,631.57	9.52	15	3.79	19.67
Sapotaceae	<i>Chrysophyllum boivinianum</i>	28	4.69	27,627.21	9.87	13	3.28	17.85
Elaeocarpaceae	<i>Sloanea rhodantha</i> var. <i>rhodantha</i>	12	2.01	38,223.33	13.66	5	1.26	16.93
Aquifoliaceae	<i>Ilex mitis</i>	31	5.19	15,641.56	5.59	19	4.80	15.58
Monimiaceae	<i>Tambourissa</i> sp2	30	5.03	10,818.00	3.87	14	3.54	12.43
Anacardiaceae	<i>Sorindeia madagascariensis</i>	33	5.53	4,735.76	1.69	18	4.55	11.77
Agavaceae	<i>Dracaena reflexa</i> ssp1	29	4.86	6,827.27	2.44	17	4.29	11.59
Lauraceae	<i>Lauraceae</i> sp3	26	4.36	8,612.66	3.08	16	4.04	11.47
Rubiaceae	<i>Hyperacanthus</i> sp1	26	4.36	7,591.27	2.71	17	4.29	11.36
Myrsinaceae	<i>Oncostemum</i> sp2	24	4.02	3,579.59	1.28	12	3.03	8.33
Myrtaceae	<i>Myrtaceae</i> sp7	16	2.68	6,112.74	2.18	10	2.53	7.39
Moraceae	<i>Moraceae</i> sp1	13	2.18	6,087.91	2.18	11	2.78	7.13
Araliaceae	<i>Polyscias</i> sp1	9	1.51	5,257.12	1.88	7	1.77	5.15
Rubiaceae	<i>Hyperacanthus</i> sp2	13	2.18	2,889.40	1.03	7	1.77	4.98
Arecaceae	<i>Dypsis</i> spp.	7	1.17	6,294.33	2.25	6	1.52	4.94
Rubiaceae	<i>Rubiaceae</i> sp2	9	1.51	7,020.09	2.51	3	0.76	4.77
Fabaceae	<i>Albizia</i> sp1	9	1.51	4,088.35	1.46	7	1.77	4.74
Rubiaceae	<i>Rubiaceae</i> sp6	10	1.68	3,077.39	1.10	5	1.26	4.04
Sapindaceae	<i>Plagioscyphus</i> sp2	3	0.50	8,158.80	2.92	2	0.51	3.92
Ebenaceae	<i>Diospyros</i> sp3	8	1.34	1,815.77	0.65	7	1.77	3.76
Elaeocarpaceae	<i>Sloanea rhodantha</i>	6	1.01	4,123.36	1.47	5	1.26	3.74
Sterculiaceae	<i>Dombeya</i> sp2	8	1.34	2,984.68	1.07	5	1.26	3.67
Cyatheaceae	<i>Cyathea</i> sp1	11	1.84	1,283.29	0.46	5	1.26	3.56
Rubiaceae	<i>Gaertnera</i> sp1	5	0.84	2,559.58	0.91	5	1.26	3.01
Euphorbiaceae	<i>Antidesma petiolare</i>	5	0.84	1,982.41	0.71	5	1.26	2.81
Annonaceae	<i>Polyalthia</i> sp1	6	1.01	772.52	0.28	6	1.52	2.80
Proteaceae	<i>Dilobeia thouarsii</i>	4	0.67	2,829.77	1.01	4	1.01	2.69
Clusiaceae	<i>Clusiaceae</i> sp1	4	0.67	2,746.18	0.98	3	0.76	2.41
Clusiaceae	<i>Clusiaceae</i> sp3	1	0.17	5,436.72	1.94	1	0.25	2.36
Annonaceae	<i>Isolona</i> sp1	6	1.01	751.34	0.27	4	1.01	2.28
Euphorbiaceae	<i>Macaranga cuspidata</i>	5	0.84	847.26	0.30	4	1.01	2.15
Flacourtiaceae	<i>Caesaria</i> sp1	5	0.84	1,539.84	0.55	3	0.76	2.15
Moraceae	<i>Treculia</i> sp1	4	0.67	1,988.33	0.71	3	0.76	2.14
Myrtaceae	<i>Eugenia emirnense</i>	3	0.50	2,425.58	0.87	3	0.76	2.13
Myrtaceae	<i>Sizygium</i> sp1	4	0.67	1,870.65	0.67	3	0.76	2.10
Clusiaceae	<i>Ochrocarpus</i> sp1	4	0.67	1,934.26	0.69	2	0.51	1.87
Lauraceae	<i>Lauraceae</i> sp4	3	0.50	1,373.16	0.49	3	0.76	1.75
Lauraceae	<i>Lauraceae</i> sp2	2	0.34	2,504.48	0.90	2	0.51	1.74
Clusiaceae	<i>Ochrocarpus</i> sp2	5	0.84	1,000.17	0.36	2	0.51	1.70
Euphorbiaceae	<i>Uapaca</i> sp1	3	0.50	2,618.57	0.94	1	0.25	1.69
Clusiaceae	<i>Clusiaceae</i> sp2	3	0.50	1,027.22	0.37	3	0.76	1.63
Sapindaceae	<i>Allophylus cobbe</i>	3	0.50	560.60	0.20	3	0.76	1.46
Euphorbiaceae	<i>Suregada</i> sp1	2	0.34	1,652.29	0.59	2	0.51	1.43
Cunoniaceae	<i>Weinmannia</i> sp1	3	0.50	1,025.24	0.37	2	0.51	1.37
Myrsinaceae	<i>Oncostemum</i> sp4	4	0.67	460.67	0.16	2	0.51	1.34
Euphorbiaceae	<i>Croton monge</i>	2	0.34	1,333.29	0.48	2	0.51	1.32
Rubiaceae	<i>Tarenna</i> sp1	3	0.50	850.44	0.30	2	0.51	1.31
Piperaceae	<i>Piper</i> sp1	3	0.50	788.06	0.28	2	0.51	1.29
Monimiaceae	<i>Tambourissa</i> sp1	3	0.50	668.51	0.24	2	0.51	1.25
Clusiaceae	<i>Mammea</i> sp2	3	0.50	639.39	0.23	2	0.51	1.24
Rubiaceae	<i>Rubiaceae</i> sp1	3	0.50	624.60	0.22	2	0.51	1.23

Appendix 4-4 Continued.

Family	Genus species	Number of individuals	Relative density (%)	Basal area (cm ²)	Relative dominance (%)	Absolute frequency	Relative frequency	IVI
Phyllanthaceae	<i>Physena madagascariensis</i>	2	0.34	1,040.20	0.37	2	0.51	1.21
Sterculiaceae	<i>Dombeya</i> sp3	2	0.34	1,028.56	0.37	2	0.51	1.21
Sterculiaceae	<i>Dombeya</i> sp5	2	0.34	950.83	0.34	2	0.51	1.18
Erythroxylaceae	<i>Erythroxylum</i> sp2	3	0.50	423.55	0.15	2	0.51	1.16
Myrsinaceae	<i>Oncostemum</i> sp6	3	0.50	404.49	0.14	2	0.51	1.15
Annonaceae	<i>Isolona</i> sp2	2	0.34	810.41	0.29	2	0.51	1.13
Myrsinaceae	<i>Oncostemum</i> sp3	3	0.50	264.99	0.09	2	0.51	1.10
Flacourtiaceae	<i>Aphloia theaeformis</i>	2	0.34	704.26	0.25	2	0.51	1.09
Lauraceae	<i>Ocotea</i> sp3	2	0.34	679.44	0.24	2	0.51	1.08
Myrtaceae	Myrtaceae sp4	1	0.17	1,809.56	0.65	1	0.25	1.07
Sapindaceae	<i>Plagioscyphus</i> sp1	2	0.34	610.99	0.22	2	0.51	1.06
Oleaceae	<i>Noronhia</i> sp1	2	0.34	417.40	0.15	2	0.51	0.99
Ebenaceae	<i>Diospyros</i> sp4	2	0.34	401.18	0.14	2	0.51	0.98
ICACINACEAE	<i>Desmatostachys</i> sp1	2	0.34	395.87	0.14	2	0.51	0.98
Ebenaceae	<i>Diospyros</i> sp2	2	0.34	330.26	0.12	2	0.51	0.96
Erythroxylaceae	<i>Erythroxylum</i> sp1	2	0.34	328.78	0.12	2	0.51	0.96
Rubiaceae	<i>Gaertnera</i> sp2	2	0.34	322.97	0.12	2	0.51	0.96
Rubiaceae	Rubiaceae sp5	2	0.34	284.17	0.10	2	0.51	0.94
Annonaceae	Annonaceae sp2	2	0.34	243.36	0.09	2	0.51	0.93
Flacourtiaceae	Flacourtiaceae sp1	2	0.34	234.52	0.08	2	0.51	0.92
Lauraceae	Lauraceae sp1	2	0.34	221.68	0.08	2	0.51	0.92
Ebenaceae	<i>Diospyros</i> sp5	2	0.34	200.72	0.07	2	0.51	0.91
Clusiaceae	<i>Garcinia</i> sp2	2	0.34	180.23	0.06	2	0.51	0.90
Cunoniaceae	<i>Weinmannia</i> sp3	3	0.50	321.06	0.11	1	0.25	0.87
Lauraceae	Lauraceae sp6	1	0.17	1,225.42	0.44	1	0.25	0.86
Lauraceae	<i>Ocotea</i> sp4	1	0.17	1,029.22	0.37	1	0.25	0.79
Euphorbiaceae	<i>Bridelia pervilleana</i>	1	0.17	956.62	0.34	1	0.25	0.76
Cunoniaceae	<i>Weinmannia</i> sp2	2	0.34	326.88	0.12	1	0.25	0.70
Rubiaceae	Rubiaceae sp3	1	0.17	518.75	0.19	1	0.25	0.61
Rubiaceae	Rubiaceae sp8	1	0.17	483.05	0.17	1	0.25	0.59
Myrtaceae	Myrtaceae sp3	1	0.17	471.44	0.17	1	0.25	0.59
Myrtaceae	Myrtaceae sp1	1	0.17	463.77	0.17	1	0.25	0.59
Sapotaceae	<i>Capurodendron</i> sp1	1	0.17	459.96	0.16	1	0.25	0.58
Rubiaceae	Rubiaceae sp4	1	0.17	373.25	0.13	1	0.25	0.55
Fabaceae	Fabaceae sp1	1	0.17	369.84	0.13	1	0.25	0.55
Rubiaceae	Rubiaceae sp7	1	0.17	369.84	0.13	1	0.25	0.55
Flacourtiaceae	Flacourtiaceae sp2	1	0.17	352.99	0.13	1	0.25	0.55
Euphorbiaceae	<i>Croton</i> sp4	1	0.17	349.67	0.12	1	0.25	0.54
Lauraceae	<i>Cinnamosma</i> sp1	1	0.17	339.80	0.12	1	0.25	0.54
Myrsinaceae	<i>Oncostemum</i> sp1	1	0.17	333.29	0.12	1	0.25	0.54
Fabaceae	Fabaceae sp2	1	0.17	330.06	0.12	1	0.25	0.54
Annonaceae	<i>Polyalthia capuronii</i>	1	0.17	326.85	0.12	1	0.25	0.54
Annonaceae	Annonaceae sp3	1	0.17	304.81	0.11	1	0.25	0.53
Clusiaceae	Clusiaceae sp4	1	0.17	304.81	0.11	1	0.25	0.53
Moraceae	<i>Strebulus dimopate</i>	1	0.17	301.72	0.11	1	0.25	0.53
Moraceae	Moraceae sp5	1	0.17	274.65	0.10	1	0.25	0.52
Rubiaceae	<i>Psychotria</i> sp1	1	0.17	243.29	0.09	1	0.25	0.51
Moraceae	Moraceae sp5	1	0.17	229.66	0.08	1	0.25	0.50
Sterculiaceae	<i>Dombeya</i> sp1	1	0.17	198.56	0.07	1	0.25	0.49
Clusiaceae	<i>Garcinia</i> sp1	1	0.17	156.15	0.06	1	0.25	0.48
Sterculiaceae	<i>Dombeya</i> sp4	1	0.17	141.03	0.05	1	0.25	0.47
Rubiaceae	Rubiaceae sp9	1	0.17	130.70	0.05	1	0.25	0.47
Myrsinaceae	<i>Oncostemum</i> sp9	1	0.17	109.36	0.04	1	0.25	0.46
Ebenaceae	<i>Diospyros</i> sp1	1	0.17	100.29	0.04	1	0.25	0.46
Monimiaceae	<i>Tambourissa</i> sp3	1	0.17	100.29	0.04	1	0.25	0.46

Appendix 4-4 Continued.

Family	Genus species	Number of individuals	Relative density (%)	Basal area (cm ²)	Relative dominance (%)	Absolute frequency	Relative frequency	IVI
Moraceae	Moraceae sp2	1	0.17	100.29	0.04	1	0.25	0.46
Lauraceae	Lauraceae sp5	1	0.17	96.77	0.03	1	0.25	0.45
Lauraceae	<i>Ocotea</i> sp1	1	0.17	95.03	0.03	1	0.25	0.45
Moraceae	Moraceae sp4	1	0.17	95.03	0.03	1	0.25	0.45
Myrsinaceae	<i>Oncostemum</i> sp5	1	0.17	95.03	0.03	1	0.25	0.45
Lauraceae	<i>Ocotea trichophebia</i>	1	0.17	89.92	0.03	1	0.25	0.45
Anacardiaceae	<i>Micronychia macrophylla</i>	1	0.17	86.59	0.03	1	0.25	0.45
Agavaceae	<i>Dracaena reflexa</i> ssp2	1	0.17	83.32	0.03	1	0.25	0.45
Myrsinaceae	<i>Oncostemum</i> sp8	1	0.17	81.71	0.03	1	0.25	0.45
Burseraceae	<i>Canarium boivinii</i>	1	0.17	80.12	0.03	1	0.25	0.45
Flacourtiaceae	Flacourtiaceae sp3	1	0.17	80.12	0.03	1	0.25	0.45
Meliaceae	<i>Turraea</i> sp1	1	0.17	80.12	0.03	1	0.25	0.45
Myrsinaceae	<i>Oncostemum</i> sp7	1	0.17	80.12	0.03	1	0.25	0.45
Annonaceae	Annonaceae sp1	1	0.17	78.54	0.03	1	0.25	0.45
Total		597	100.00	279,800.69	100.00	395	99.75	299.75

Plot 2 at 840 m

Family	Genus species	Number of individuals	Relative density (%)	Basal area (cm ²)	Relative dominance (%)	Absolute frequency	Relative frequency	IVI
Elaeocarpaceae	<i>Sloanea rhodantha</i>	40	5.14	54,610.72	14.10	18	3.35	22.60
Araliaceae	<i>Polyscias</i> sp1	23	2.96	12,474.13	3.22	14	2.61	8.78
Myrtaceae	Myrtaceae sp11	24	3.08	10,031.35	2.59	15	2.79	8.47
Lauraceae	<i>Ocotea</i> sp1	18	2.31	15,719.07	4.06	11	2.05	8.42
Moraceae	<i>Streblus dimepate</i>	27	3.47	4,197.67	1.08	16	2.98	7.53
Moraceae	Moraceae sp1	7	0.90	21,099.64	5.45	6	1.12	7.47
Euphorbiaceae	<i>Macaranga</i> sp1	28	3.60	6,809.20	1.76	11	2.05	7.41
Monimiaceae	<i>Tambourissa</i> sp1	22	2.83	6,078.97	1.57	14	2.61	7.00
Bignoniaceae	<i>Ophiocolea floribunda</i>	20	2.57	7,985.05	2.06	12	2.23	6.87
Monimiaceae	<i>Tambourissa</i> sp2	20	2.57	8,461.82	2.19	11	2.05	6.80
Annonaceae	Annonaceae sp1	8	1.03	16,491.53	4.26	6	1.12	6.40
Aquifoliaceae	<i>Ilex mitis</i>	18	2.31	7,711.92	1.99	11	2.05	6.35
Flacourtiaceae	Flacourtiaceae sp1	21	2.70	4,150.26	1.07	12	2.23	6.01
Myrtaceae	Myrtaceae sp1	13	1.67	9,924.81	2.56	8	1.49	5.72
Myrtaceae	Myrtaceae sp9	15	1.93	7,659.19	1.98	9	1.68	5.58
Cunoniaceae	<i>Weinmannia</i> sp5	15	1.93	11,908.14	3.08	3	0.56	5.56
Ebenaceae	<i>Diospyros</i> sp3	11	1.41	8,811.35	2.28	10	1.86	5.55
Annonaceae	Annonaceae sp2	15	1.93	5,565.35	1.44	11	2.05	5.41
Rubiaceae	Rubiaceae sp1	13	1.67	7,526.73	1.94	6	1.12	4.73
Cyatheaceae	<i>Cyathea</i> sp1	14	1.80	4,450.01	1.15	9	1.68	4.62
Anacardiaceae	Anacardiaceae sp4	10	1.29	7,872.42	2.03	7	1.30	4.62
Cunoniaceae	<i>Weinmannia</i> sp3	17	2.19	4,799.53	1.24	5	0.93	4.36
Oleaceae	<i>Noronhia</i> sp2	13	1.67	3,749.56	0.97	9	1.68	4.32
Flacourtiaceae	<i>Scolopia</i> sp1	10	1.29	5,706.28	1.47	8	1.49	4.25
Fabaceae	Fabaceae sp1	12	1.54	4,175.62	1.08	7	1.30	3.92
Proteaceae	<i>Dilobeia thouarsii</i>	6	0.77	7,079.89	1.83	6	1.12	3.72
Clusiaceae	Clusiaceae sp2	11	1.41	2,193.37	0.57	9	1.68	3.66
Clusiaceae	<i>Mammea</i> sp3	9	1.16	2,567.97	0.66	8	1.49	3.31
Rubiaceae	<i>Breonia</i> sp1	9	1.16	4,422.53	1.14	5	0.93	3.23
Monimiaceae	<i>Tambourissa</i> sp5	10	1.29	2,307.87	0.60	7	1.30	3.18
Agavaceae	<i>Dracaena reflexa</i> ssp1	6	0.77	6,156.32	1.59	4	0.74	3.11
Flacourtiaceae	<i>Tisonia</i> sp1	4	0.51	8,501.73	2.20	2	0.37	3.08

Appendix 4-4 Continued.

Family	Genus species	Number of individuals	Relative density (%)	Basal area (cm ²)	Relative dominance (%)	Absolute frequency	Relative frequency	IVI
Euphorbiaceae	<i>Drypetes madagascariensis</i>	8	1.03	2,481.87	0.64	6	1.12	2.79
Monimiaceae	<i>Tambourissa</i> sp3	8	1.03	2,818.28	0.73	5	0.93	2.69
Rutaceae	<i>Zanthoxylum</i> sp1	7	0.90	2,543.17	0.66	6	1.12	2.67
Clusiaceae	<i>Ochrocarpus</i> sp2	9	1.16	1,408.49	0.36	6	1.12	2.64
Flacourtiaceae	<i>Caesaria</i> sp1	6	0.77	2,245.23	0.58	6	1.12	2.47
Lauraceae	<i>Cryptocarya</i> sp1	5	0.64	3,167.84	0.82	5	0.93	2.39
Moraceae	Moraceae sp2	6	0.77	2,547.42	0.66	5	0.93	2.36
Cunoniaceae	<i>Weinmannia</i> sp1	10	1.29	1,643.13	0.42	3	0.56	2.27
Moraceae	<i>Trilepisium madagascariensis</i>	7	0.90	918.95	0.24	5	0.93	2.07
Moraceae	<i>Streblus mauritanus</i>	6	0.77	1,231.01	0.32	5	0.93	2.02
Euphorbiaceae	<i>Bridelia tulasneana</i>	4	0.51	3,575.07	0.92	3	0.56	2.00
Euphorbiaceae	<i>Croton monge</i>	4	0.51	2,684.76	0.69	4	0.74	1.95
Monimiaceae	<i>Tambourissa</i> sp4	6	0.77	1,349.22	0.35	4	0.74	1.86
Sterculiaceae	<i>Dombeya</i> sp4	2	0.26	4,596.42	1.19	2	0.37	1.82
Moraceae	<i>Streblus</i> sp1	4	0.51	2,079.59	0.54	4	0.74	1.80
Lauraceae	<i>Cryptocarya</i> sp2	3	0.39	2,586.70	0.67	3	0.56	1.61
Araliaceae	<i>Schefflera</i> sp1	5	0.64	1,585.95	0.41	3	0.56	1.61
Araliaceae	<i>Polyscias</i> sp10	4	0.51	1,331.56	0.34	4	0.74	1.60
Cunoniaceae	<i>Weinmannia</i> sp2	5	0.64	591.51	0.15	4	0.74	1.54
Clusiaceae	Clusiaceae sp4	4	0.51	1,069.37	0.28	4	0.74	1.54
Araliaceae	<i>Polyscias</i> sp10	5	0.64	1,078.78	0.28	3	0.56	1.48
Rutaceae	<i>Vepris</i> sp4	3	0.39	1,787.20	0.46	3	0.56	1.41
Araliaceae	<i>Schefflera</i> sp3	6	0.77	1,648.75	0.43	1	0.19	1.38
Rubiaceae	Rubiaceae sp7	4	0.51	1,040.98	0.27	3	0.56	1.34
Melastomataceae	<i>Mennecylon</i> sp1	3	0.39	2,241.13	0.58	2	0.37	1.34
Rubiaceae	Rubiaceae sp2	3	0.39	1,502.77	0.39	3	0.56	1.33
Myrsinaceae	<i>Oncostemum</i> sp10	3	0.39	1,398.92	0.36	3	0.56	1.31
Verbenaceae	<i>Vitex</i> sp5	4	0.51	808.32	0.21	3	0.56	1.28
Myrtaceae	Myrtaceae sp2	3	0.39	1,236.10	0.32	3	0.56	1.26
Euphorbiaceae	<i>Macaranga</i> sp3	4	0.51	601.72	0.16	3	0.56	1.23
Sterculiaceae	<i>Dombeya</i> sp5	2	0.26	2,094.14	0.54	2	0.37	1.17
Rubiaceae	<i>Psychotria</i> sp1	3	0.39	869.72	0.22	3	0.56	1.17
Elaeocarpaceae	<i>Elaeocarpus</i> sp1	3	0.39	697.66	0.18	3	0.56	1.12
Fabaceae	<i>Albizia gumifera</i>	3	0.39	696.15	0.18	3	0.56	1.12
Flacourtiaceae	Flacourtiaceae sp2	2	0.26	1,832.40	0.47	2	0.37	1.10
Euphorbiaceae	<i>Bridelia pervilleana</i>	3	0.39	588.15	0.15	3	0.56	1.10
Rubiaceae	<i>Gaertnera</i> sp2	3	0.39	543.09	0.14	3	0.56	1.08
Agavaceae	<i>Dracaena reflexa</i> ssp2	3	0.39	508.58	0.13	3	0.56	1.08
Clusiaceae	<i>Ochrocarpus</i> sp1	3	0.39	454.22	0.12	3	0.56	1.06
Meliaceae	<i>Malleastrum gracile</i>	3	0.39	445.64	0.12	3	0.56	1.06
Lauraceae	Lauraceae sp8	2	0.26	1,644.54	0.42	2	0.37	1.05
Monimiaceae	<i>Tambourissa</i> sp6	3	0.39	414.88	0.11	3	0.56	1.05
Clusiaceae	<i>Garcinia</i> sp1	2	0.26	1,629.31	0.42	2	0.37	1.05
Rubiaceae	Rubiaceae sp11	3	0.39	405.99	0.10	3	0.56	1.05
Rubiaceae	Rubiaceae sp5	2	0.26	1,579.23	0.41	2	0.37	1.04
Verbenaceae	<i>Clerodendrum</i> sp1	2	0.26	1,465.97	0.38	2	0.37	1.01
Lauraceae	<i>Ocotea</i> sp2	3	0.39	944.87	0.24	2	0.37	1.00
Pittosporaceae	<i>Pittosporum</i> sp1	2	0.26	1,383.79	0.36	2	0.37	0.99
Araliaceae	<i>Polyscias</i> sp5	3	0.39	610.08	0.16	2	0.37	0.92
Verbenaceae	<i>Vitex</i> sp3	2	0.26	1,028.44	0.27	2	0.37	0.90
Sapindaceae	Sapindaceae sp1	2	0.26	1,024.94	0.26	2	0.37	0.89
Araliaceae	Araliaceae sp1	3	0.39	496.01	0.13	2	0.37	0.89
Ebenaceae	<i>Diospyros</i> sp1	2	0.26	864.76	0.22	2	0.37	0.85
Sapindaceae	<i>Allophylus</i> sp1	2	0.26	826.77	0.21	2	0.37	0.84
Moraceae	Moraceae sp7	2	0.26	781.08	0.20	2	0.37	0.83
Euphorbiaceae	<i>Macaranga</i> sp2	2	0.26	731.94	0.19	2	0.37	0.82

Appendix 4-4 Continued.

Family	Genus species	Number of individuals	Relative density (%)	Basal area (cm ²)	Relative dominance (%)	Absolute frequency	Relative frequency	IVI
Rubiaceae	Rubiaceae sp6	2	0.26	448.89	0.12	2	0.37	0.75
Lauraceae	Lauraceae sp5	2	0.26	349.61	0.09	2	0.37	0.72
Myrtaceae	Myrtaceae sp3	2	0.26	338.77	0.09	2	0.37	0.72
Moraceae	<i>Ficus</i> sp2	2	0.26	322.91	0.08	2	0.37	0.71
Ebenaceae	<i>Diospyros</i> sp2	2	0.26	321.27	0.08	2	0.37	0.71
Sterculiaceae	<i>Dombeya</i> sp2	2	0.26	309.78	0.08	2	0.37	0.71
Clusiaceae	<i>Mammea</i> sp1	2	0.26	272.85	0.07	2	0.37	0.70
Sterculiaceae	<i>Dombeya</i> sp1	2	0.26	268.80	0.07	2	0.37	0.70
Moraceae	Moraceae sp8	2	0.26	264.80	0.07	2	0.37	0.70
Anacardiaceae	Anacardiaceae sp3	2	0.26	202.15	0.05	2	0.37	0.68
Anacardiaceae	<i>Protorhus</i> sp1	1	0.26	1,418.63	0.37	1	0.19	0.68
Moraceae	Moraceae sp4	2	0.13	186.05	0.05	2	0.37	0.68
Rubiaceae	<i>Psychotria</i> sp2	2	0.26	185.11	0.05	2	0.37	0.68
Pandanaceae	<i>Pandanus</i> sp3	2	0.26	165.13	0.04	2	0.37	0.67
Clusiaceae	<i>Harungana</i> sp1	1	0.13	1,372.28	0.35	1	0.19	0.67
Anacardiaceae	Anacardiaceae sp5	2	0.26	555.03	0.14	1	0.19	0.59
Araliaceae	<i>Polyscias</i> sp4	1	0.13	1,023.54	0.26	1	0.19	0.58
Ebenaceae	<i>Diospyros</i> sp4	2	0.26	234.19	0.06	1	0.19	0.50
Clusiaceae	Clusiaceae sp3	1	0.13	543.25	0.14	1	0.19	0.46
Clusiaceae	Clusiaceae sp1	1	0.13	433.74	0.11	1	0.19	0.43
Sterculiaceae	<i>Dombeya</i> sp3	1	0.13	411.87	0.11	1	0.19	0.42
Bignoniaceae	<i>Rhodocolea linearis</i>	1	0.13	408.28	0.11	1	0.19	0.42
Oleaceae	<i>Noronhia</i> sp3	1	0.13	359.68	0.09	1	0.19	0.41
Clusiaceae	<i>Ochrocarpus</i> sp3	1	0.13	311.03	0.08	1	0.19	0.40
Arecaceae	<i>Dypsis</i> sp1	1	0.13	298.65	0.08	1	0.19	0.39
Myrtaceae	Myrtaceae sp8	1	0.13	268.80	0.07	1	0.19	0.38
Verbenaceae	<i>Vitex</i> sp1	1	0.13	268.80	0.07	1	0.19	0.38
Moraceae	Moraceae sp9	1	0.13	260.16	0.07	1	0.19	0.38
Clusiaceae	<i>Garcinia</i> sp2	1	0.13	229.66	0.06	1	0.19	0.37
Lauraceae	<i>Cryptocarya</i> sp4	1	0.13	221.67	0.06	1	0.19	0.37
Lauraceae	Lauraceae sp2	1	0.13	201.06	0.05	1	0.19	0.37
Rubiaceae	<i>Craterispermum</i> sp1	1	0.13	201.06	0.05	1	0.19	0.37
Apocynaceae	<i>Cabucala</i> sp1	1	0.13	191.13	0.05	1	0.19	0.36
Moraceae	<i>Streblus</i> sp2	1	0.13	174.37	0.05	1	0.19	0.36
Araliaceae	<i>Gastonia</i> sp1	1	0.13	153.94	0.04	1	0.19	0.35
Moraceae	Moraceae sp3	1	0.13	153.94	0.04	1	0.19	0.35
Moraceae	<i>Trophis montana</i>	1	0.13	138.93	0.04	1	0.19	0.35
Tiliaceae	<i>Grewia</i> sp2	1	0.13	136.85	0.04	1	0.19	0.35
Myrtaceae	Myrtaceae sp5	1	0.13	128.68	0.03	1	0.19	0.35
Monimiaceae	<i>Decarydendron</i> sp1	1	0.13	126.68	0.03	1	0.19	0.35
Cyatheaceae	<i>Cyathea</i> sp2	1	0.13	122.72	0.03	1	0.19	0.35
Euphorbiaceae	<i>Drypetes</i> sp2	1	0.13	122.72	0.03	1	0.19	0.35
Moraceae	Moraceae sp6	1	0.13	122.72	0.03	1	0.19	0.35
Anacardiaceae	Anacardiaceae sp1	1	0.13	120.76	0.03	1	0.19	0.35
Elaeocarpaceae	<i>Elaeocarpus</i> sp6	1	0.13	120.76	0.03	1	0.19	0.35
Tiliaceae	<i>Grewia</i> sp1	1	0.13	113.10	0.03	1	0.19	0.34
Annonaceae	<i>Xylopia</i> sp1	1	0.13	109.36	0.03	1	0.19	0.34
Myrtaceae	Myrtaceae sp10	1	0.13	103.87	0.03	1	0.19	0.34
Burseraceae	<i>Canarium</i> sp1	1	0.13	100.29	0.03	1	0.19	0.34
Annonaceae	Annonaceae sp4	1	0.13	98.52	0.03	1	0.19	0.34
Apocynaceae	<i>Landolphia</i> sp1	1	0.13	98.52	0.03	1	0.19	0.34
Moraceae	<i>Ficus soroceoides</i>	1	0.13	95.03	0.02	1	0.19	0.34
Monimiaceae	Monimiaceae sp3	1	0.13	91.61	0.02	1	0.19	0.34
Euphorbiaceae	Euphorbiaceae sp1	1	0.13	84.95	0.02	1	0.19	0.34
Lauraceae	<i>Cryptocarya</i> sp3	1	0.13	84.95	0.02	1	0.19	0.34
Meliaceae	<i>Malleastrum</i> sp2	1	0.13	81.71	0.02	1	0.19	0.34
Monimiaceae	Monimiaceae sp2	1	0.13	80.12	0.02	1	0.19	0.34
Annonaceae	Annonaceae sp5	1	0.13	78.54	0.02	1	0.19	0.34
Total		778	100.00	387,254.80	100.00	537	100.00	300.00

Appendix 4-4 Continued.

Plot 3 at 1150 m

Family	Genus species	Number of individuals	Relative density (%)	Basal area (cm ²)	Relative dominance (%)	Absolute frequency	Relative frequency	IVI
Sterculiaceae	<i>Dombeya</i> sp9	42	3.72	55,482.83	12.70	13	1.95	18.38
Myrtaceae	Myrtaceae sp13	92	8.15	23,539.12	5.39	23	3.46	17.00
Myrtaceae	Myrtaceae sp14	54	4.78	23,573.35	5.40	23	3.46	13.64
Moraceae	<i>Trilepisium</i> <i>madagascariensis</i>	74	6.55	17,628.14	4.04	17	2.56	13.15
Lauraceae	Lauraceae sp10	52	4.61	19,719.64	4.52	20	3.01	12.13
Elaeocarpaceae	<i>Sloanea rhodantha</i>	38	3.37	23,186.55	5.31	21	3.16	11.83
Sterculiaceae	<i>Dombeya</i> sp3	37	3.28	13,178.82	3.02	22	3.31	9.60
Monimiaceae	<i>Tambourissa</i> sp7	49	4.34	8,348.30	1.91	18	2.71	8.96
Aquifoliaceae	<i>Ilex mitis</i>	29	2.57	16,693.73	3.82	17	2.56	8.95
Monimiaceae	<i>Tambourissa</i> sp4	15	1.33	25,410.51	5.82	10	1.50	8.65
Sapindaceae	<i>Allophylus</i> sp2	34	3.01	9,972.92	2.28	21	3.16	8.45
Sapotaceae	<i>Chrysophyllum</i> <i>boivinianum</i>	21	1.86	13,999.02	3.21	12	1.80	6.87
Lauraceae	Lauraceae sp14	23	2.04	12,134.87	2.78	12	1.80	6.62
Lauraceae	Lauraceae sp12	17	1.51	11,472.39	2.63	12	1.80	5.94
Lauraceae	Lauraceae sp9	19	1.68	7,954.79	1.82	15	2.26	5.76
Araliaceae	<i>Polyscias</i> sp1	22	1.95	8,355.90	1.91	12	1.80	5.67
Lauraceae	Lauraceae sp13	15	1.33	11,698.17	2.68	10	1.50	5.51
Clusiaceae	<i>Mammea</i> sp1	21	1.86	6,400.68	1.47	12	1.80	5.13
Rubiaceae	<i>Gaertnera</i> sp4	29	2.57	3,608.46	0.83	11	1.65	5.05
Arecaceae	<i>Dypsis</i> spp	19	1.68	7,237.66	1.66	11	1.65	4.99
Annonaceae	<i>Polyalthia</i> sp1	19	1.68	4,455.78	1.02	13	1.95	4.66
Lauraceae	<i>Cryptocarya</i> sp1	18	1.59	5,749.63	1.32	10	1.50	4.41
Elaeocarpaceae	<i>Elaeocarpus</i> sp5	17	1.51	2,819.92	0.65	12	1.80	3.96
Tiliaceae	<i>Grewia</i> sp1	14	1.24	3,189.71	0.73	12	1.80	3.77
Myrtaceae	Myrtaceae sp8	19	1.68	6,117.29	1.40	2	0.30	3.38
Moraceae	<i>Ficus</i> sp2	5	0.44	10,426.27	2.39	3	0.45	3.28
Euphorbiaceae	<i>Croton monge</i>	10	0.89	4,480.96	1.03	9	1.35	3.27
Loganiaceae	<i>Anthocleista</i> <i>madagascariensis</i>	11	0.97	3,070.26	0.70	8	1.20	2.88
Myrtaceae	Myrtaceae sp12	12	1.06	2,265.36	0.52	8	1.20	2.78
Meliaceae	<i>Malleastrum gracile</i>	13	1.15	1,860.26	0.43	7	1.05	2.63
Sterculiaceae	<i>Dombeya</i> sp7	9	0.80	3,325.72	0.76	7	1.05	2.61
Cyatheaceae	<i>Cyathea</i> sp1	9	0.80	1,161.74	0.27	9	1.35	2.42
Myrtaceae	Myrtaceae sp5	3	0.27	1,921.71	0.44	11	1.65	2.36
Anacardiaceae	<i>Micronychia</i> <i>macrophylla</i>	11	0.97	1,425.50	0.33	7	1.05	2.35
Verbenaceae	<i>Vitex</i> sp6	9	0.80	1,915.74	0.44	7	1.05	2.29
Monimiaceae	<i>Tambourissa</i> sp2	8	0.71	2,001.90	0.46	6	0.90	2.07
Euphorbiaceae	<i>Croton</i> sp1	9	0.80	1,182.39	0.27	6	0.90	1.97
Verbenaceae	<i>Vitex</i> sp1	7	0.62	1,091.11	0.25	7	1.05	1.92
Euphorbiaceae	Euphorbiaceae sp2	2	0.18	318.59	0.07	11	1.65	1.90
Rubiaceae	<i>Gaertnera</i> sp3	8	0.71	1,534.73	0.35	5	0.75	1.81
Ebenaceae	<i>Diospyros</i> sp2	7	0.62	1,912.83	0.44	5	0.75	1.81
Moraceae	<i>Ficus</i> sp4	3	0.27	4,762.85	1.09	3	0.45	1.81
Myrsinaceae	<i>Memecylon</i> sp1	5	0.44	2,509.21	0.57	5	0.75	1.77
Sapindaceae	Sapindaceae sp1	5	0.44	2,699.81	0.62	4	0.60	1.66
Lauraceae	Lauraceae sp1	5	0.44	2,332.67	0.53	4	0.60	1.58
Rubiaceae	Rubiaceae sp3	7	0.62	897.93	0.21	5	0.75	1.58
Icacinaceae	Icacinaceae sp1	4	0.35	3,981.43	0.91	2	0.30	1.57
Cunoniaceae	<i>Weinmannia</i> sp6	5	0.44	594.16	0.14	5	0.75	1.33
Euphorbiaceae	<i>Antidesma</i> sp1	5	0.44	558.97	0.13	5	0.75	1.32
Meliaceae	<i>Malleastrum</i> sp3	5	0.44	991.13	0.23	4	0.60	1.27
Moraceae	Moraceae sp2	4	0.35	1,332.43	0.31	4	0.60	1.26
Anacardiaceae	Anacardiaceae sp2	4	0.35	1,227.09	0.28	4	0.60	1.24
Araliaceae	<i>Schefflera</i> sp1	3	0.27	2,897.29	0.66	2	0.30	1.23
Myrsinaceae	<i>Oncostemum</i> sp3	5	0.44	536.73	0.12	4	0.60	1.17
Apocynaceae	Apocynaceae sp2	4	0.35	886.05	0.20	4	0.60	1.16
Lauraceae	<i>Ocotea</i> sp1	4	0.35	1,357.52	0.31	3	0.45	1.12

Appendix 4-4 Continued.

Plot 3 at 1150 m

Family	Genus species	Number of individuals	Relative density (%)	Basal area (cm ²)	Relative dominance (%)	Absolute frequency	Relative frequency	IVI
Pandanaceae	<i>Pandanus</i> sp2	4	0.35	649.50	0.15	4	0.60	1.10
Hamamelidaceae	<i>Dicoryphe</i> sp1	4	0.35	615.10	0.14	4	0.60	1.10
Araliaceae	<i>Polyscias</i> sp2	4	0.35	1,185.40	0.27	3	0.45	1.08
Connaraceae	<i>Ellipanthus</i> sp1	3	0.27	1,517.17	0.35	3	0.45	1.06
Oleaceae	<i>Noronhia</i> sp5	4	0.35	1,100.30	0.25	3	0.45	1.06
Ebenaceae	<i>Diospyros</i> sp1	4	0.35	393.71	0.09	4	0.60	1.05
Flacourtiaceae	<i>Scolopia</i> sp1	4	0.35	392.91	0.09	4	0.60	1.05
Euphorbiaceae	<i>Phyllanthus</i> sp1	4	0.35	741.18	0.17	3	0.45	0.98
Araliaceae	<i>Polyscias</i> sp4	3	0.27	1,008.25	0.23	3	0.45	0.95
Elaeocarpaceae	<i>Elaeocarpus</i> sp2	3	0.27	944.84	0.22	3	0.45	0.93
Euphorbiaceae	<i>Macaranga</i> sp1	4	0.35	474.45	0.11	3	0.45	0.91
Pittosporaceae	<i>Pittosporum</i> sp1	4	0.35	460.33	0.11	3	0.45	0.91
Sterculiaceae	<i>Sterculiaceae</i> sp1	4	0.35	428.48	0.10	3	0.45	0.90
Araliaceae	<i>Polyscias</i> sp3	3	0.27	743.21	0.17	3	0.45	0.89
Araliaceae	<i>Schefflera</i> sp4	3	0.27	563.76	0.13	3	0.45	0.85
Cunoniaceae	<i>Weinmannia</i> sp4	3	0.27	1,199.66	0.27	2	0.30	0.84
Anacardiaceae	<i>Anacardiaceae</i> sp3	2	0.18	923.79	0.21	3	0.45	0.84
Rubiaceae	<i>Rubiaceae</i> sp13	3	0.27	515.85	0.12	3	0.45	0.83
Sterculiaceae	<i>Dombeya</i> sp6	3	0.27	489.50	0.11	3	0.45	0.83
Euphorbiaceae	<i>Macaranga</i> sp2	3	0.27	477.66	0.11	3	0.45	0.83
Euphorbiaceae	<i>Antidesma petiolare</i>	3	0.27	400.73	0.09	3	0.45	0.81
Rubiaceae	<i>Rubiaceae</i> sp2	4	0.35	548.01	0.13	2	0.30	0.78
Lauraceae	<i>Lauraceae</i> sp8	2	0.18	678.44	0.16	2	0.30	0.63
Rubiaceae	<i>Rubiaceae</i> sp9	2	0.18	600.77	0.14	2	0.30	0.62
Burseraceae	<i>Canarium boivianum</i>	2	0.18	580.69	0.13	2	0.30	0.61
Ebenaceae	<i>Diospyros</i> sp6	2	0.18	467.98	0.11	2	0.30	0.59
Oleaceae	<i>Noronhia</i> sp1	2	0.18	531.13	0.10	2	0.30	0.58
Rubiaceae	<i>Psychotria</i> sp3	2	0.18	357.71	0.08	2	0.30	0.56
Rutaceae	<i>Zanthoxylum</i> sp1	2	0.18	344.08	0.08	2	0.30	0.56
Sapindaceae	<i>Macphersonia</i> sp1	2	0.18	278.23	0.06	2	0.30	0.54
Myrsinaceae	<i>Oncostemum</i> sp4	2	0.18	265.86	0.06	2	0.30	0.54
Euphorbiaceae	<i>Drypetes</i> sp3	2	0.18	224.32	0.05	2	0.30	0.53
Rubiaceae	<i>Psychotria</i> sp4	2	0.18	223.44	0.05	2	0.30	0.53
Rubiaceae	<i>Rubiaceae</i> sp12	2	0.18	218.56	0.05	2	0.30	0.53
Euphorbiaceae	<i>Drypetes madagascariensis</i>	2	0.18	214.61	0.05	2	0.30	0.53
Rubiaceae	<i>Rubiaceae</i> sp10	2	0.18	188.82	0.04	2	0.30	0.52
Moraceae	<i>Ficus</i> sp1	1	0.09	886.68	0.20	1	0.15	0.44
Myrtaceae	<i>Myrtaceae</i> sp4	2	0.18	262.61	0.06	1	0.15	0.39
Rubiaceae	<i>Psychotria</i> sp5	1	0.09	369.84	0.08	1	0.15	0.32
Anacardiaceae	<i>Protorhus</i> sp2	1	0.09	330.06	0.08	1	0.15	0.31
Sapotaceae	<i>Sapotaceae</i> sp1	1	0.09	298.65	0.07	1	0.15	0.31
Oleaceae	<i>Noronhia</i> sp4	1	0.09	280.55	0.06	1	0.15	0.30
Rubiaceae	<i>Rothmania</i> sp1	1	0.09	248.85	0.06	1	0.15	0.30
Annonaceae	<i>Annonaceae</i> sp2	1	0.09	240.53	0.06	1	0.15	0.29
Violaceae	<i>Rinorea</i> sp1	1	0.09	226.98	0.05	1	0.15	0.29
Rutaceae	<i>Vepris</i> sp4	1	0.09	219.04	0.05	1	0.15	0.29
Sapotaceae	<i>Minusops</i> sp1	1	0.09	203.58	0.05	1	0.15	0.29
Lauraceae	<i>Lauraceae</i> sp7	1	0.09	201.06	0.05	1	0.15	0.28
Loganiaceae	<i>Loganiaceae</i> sp1	1	0.09	162.86	0.04	1	0.15	0.28
Apocynaceae	<i>Apocynaceae</i> sp1	1	0.09	156.15	0.04	1	0.15	0.27
Myrtaceae	<i>Myrtaceae</i> sp6	1	0.09	153.94	0.04	1	0.15	0.27
Rutaceae	<i>Vepris</i> sp5	1	0.09	153.94	0.04	1	0.15	0.27
Rubiaceae	<i>Psychotria</i> sp1	1	0.09	149.57	0.03	1	0.15	0.27

Appendix 4-4 Continued.

Family	Genus species	Number of individuals	Relative density (%)	Basal area (cm ²)	Relative dominance (%)	Absolute frequency	Relative frequency	IVI
Euphorbiaceae	<i>Phyllanthus</i> sp2	1	0.09	147.41	0.03	1	0.15	0.27
Flacourtiaceae	<i>Tisonia</i> sp2	1	0.09	147.41	0.03	1	0.15	0.27
Agavaceae	<i>Dracaena reflexa</i> ssp1	1	0.09	143.14	0.03	1	0.15	0.27
Anacardiaceae	Anacardiaceae sp4	1	0.09	136.85	0.03	1	0.15	0.27
Moraceae	<i>Ficus</i> sp3	1	0.09	134.78	0.03	1	0.15	0.27
Verbenaceae	<i>Vitex</i> sp2	1	0.09	118.82	0.03	1	0.15	0.27
Euphorbiaceae	<i>Croton</i> sp5	1	0.09	116.90	0.03	1	0.15	0.27
Rutaceae	<i>Vepris</i> sp3	1	0.09	114.99	0.03	1	0.15	0.27
Annonaceae	<i>Xylopia</i> sp2	1	0.09	109.36	0.03	1	0.15	0.26
Flacourtiaceae	<i>Tisonia</i> sp1	1	0.09	107.51	0.02	1	0.15	0.26
Euphorbiaceae	<i>Drypoetes</i> sp1	1	0.09	102.07	0.02	1	0.15	0.26
Clusiaceae	<i>Ochrocarpus</i> sp4	1	0.09	93.31	0.02	1	0.15	0.26
Fabaceae	Fabaceae sp3	1	0.09	93.31	0.02	1	0.15	0.26
Monimiaceae	Monimiaceae sp2	1	0.09	93.31	0.02	1	0.15	0.26
Bignoniaceae	<i>Colea</i> sp1	1	0.09	91.61	0.02	1	0.15	0.26
Verbenaceae	<i>Clerodendrum</i> sp1	1	0.09	86.59	0.02	1	0.15	0.26
Flacourtiaceae	<i>Aphloia theaeformis</i>	1	0.09	84.95	0.02	1	0.15	0.26
Total		1,129	100.00	436,704.16	100.00	665	100.00	300.00

Plot 4 at 1550 m

Family	Genus species	Number of individuals	Relative density (%)	Basal area (cm ²)	Relative dominance (%)	Absolute frequency	Relative frequency	IVI
Elaeocarpaceae	<i>Sloanea rhodantha</i> var. <i>quercifolia</i>	3	0.48	204,780.58	33.77	3	0.87	35.13
Euphorbiaceae	<i>Macaranga</i> sp2	95	15.25	29,016.73	4.79	25	7.27	27.30
Elaeocarpaceae	<i>Sloanea rhodantha</i> var. <i>rhodantha</i>	22	3.53	92,198.87	15.21	14	4.07	22.81
Lauraceae	Lauraceae sp10	66	10.59	20,897.65	3.45	23	6.69	20.73
Monimiaceae	Monimiaceae sp1	40	6.42	34,282.75	5.65	23	6.69	18.76
Cunoniaceae	<i>Weinmannia</i> sp4	42	6.74	23,366.65	3.85	17	4.94	15.54
Cyatheaceae	<i>Cyathea</i> sp1	41	6.58	7,224.38	1.19	16	4.65	12.42
Meliaceae	<i>Malleastrum</i> sp1	27	4.33	24,068.97	3.97	14	4.07	12.37
Lauraceae	Lauraceae sp15	16	2.57	22,567.43	3.72	11	3.20	9.49
Sterculiaceae	<i>Dombeya</i> sp2	23	3.69	10,069.28	1.66	14	4.07	9.42
Araliaceae	<i>Polyscias</i> sp9	23	3.69	13,967.25	2.30	4	1.16	7.16
Myrtaceae	Myrtaceae sp15	12	1.93	12,552.64	2.07	9	2.62	6.61
Monimiaceae	<i>Tambourissa</i> sp1	7	1.12	19,905.00	3.28	7	2.03	6.44
Sterculiaceae	<i>Dombeya</i> sp9	11	1.77	9,496.62	1.57	7	2.03	5.37
Sterculiaceae	<i>Dombeya</i> sp1	14	2.25	5,083.07	0.84	6	1.74	4.83
Clusiaceae	<i>Mammea</i> sp1	13	2.09	4,045.46	0.67	7	2.03	4.79
Sterculiaceae	<i>Dombeya</i> sp5	9	1.44	7,144.77	1.18	7	2.03	4.66
Hamamelidaceae	<i>Dicoryphe</i> sp1	9	1.44	6,853.60	1.13	6	1.74	4.32
Myrtaceae	Myrtaceae sp16	7	1.12	7,697.13	1.27	5	1.45	3.85
Clusiaceae	<i>Ochrocarpus</i> sp4	10	1.61	2,307.57	0.38	6	1.74	3.73
Euphorbiaceae	<i>Croton</i> sp1	9	1.44	1,437.57	0.24	7	2.03	3.72
Lauraceae	<i>Potameia</i> sp1	6	0.96	6,905.53	1.14	5	1.45	3.56
Fabaceae	<i>Stronglyodon</i> sp1	8	1.28	1,230.35	0.20	7	2.03	3.52
Sterculiaceae	<i>Dombeya</i> sp11	7	1.12	2,823.89	0.47	6	1.74	3.33
Araliaceae	<i>Polyscias</i> sp8	2	0.32	223.71	0.04	10	2.91	3.26
Agavaceae	<i>Dracaena reflexa</i> ssp1	7	1.12	909.27	0.15	6	1.74	3.02
Pandanaceae	<i>Pandanus</i> sp1	7	1.12	1,062.36	0.18	5	1.45	2.75
Sterculiaceae	<i>Dombeya</i> sp10	8	1.28	1,668.59	0.28	4	1.16	2.72

Appendix 4-4 Continued.

Family	Genus species	Number of individuals	Relative density (%)	Basal area (cm ²)	Relative dominance (%)	Absolute frequency	Relative frequency	IVI
Flacourtiaceae	<i>Aphloia theaeiformis</i>	7	1.12	2,004.74	0.33	4	1.16	2.62
Monimiaceae	Monimiaceae sp2	5	0.80	3,038.97	0.50	4	1.16	2.47
Rubiaceae	Rubiaceae sp15	5	0.80	936.27	0.15	5	1.45	2.41
Clusiaceae	<i>Ochrocarpus</i> sp1	4	0.64	2,769.58	0.46	4	1.16	2.26
Clusiaceae	<i>Symphonia</i> sp1	4	0.64	1,840.36	0.30	4	1.16	2.11
Myrsinaceae	<i>Oncostemum</i> sp8	4	0.64	677.19	0.11	4	1.16	1.92
Arecaceae	<i>Dypsis</i> spp	3	0.48	1,570.40	0.26	3	0.87	1.61
Rubiaceae	<i>Schysmatoclada</i> sp1	3	0.48	288.75	0.05	3	0.87	1.40
Araliaceae	<i>Polyscias</i> sp6	5	0.80	1,134.11	0.19	1	0.29	1.28
Lauraceae	Lauraceae sp4	2	0.32	1,790.37	0.30	2	0.58	1.20
Lauraceae	Lauraceae sp11	1	0.16	3,728.45	0.61	1	0.29	1.07
Rubiaceae	<i>Ixora</i> sp1	2	0.32	950.34	0.16	2	0.58	1.06
Rhizophoraceae	Rhizophoraceae sp1	1	0.16	3,599.71	0.59	1	0.29	1.04
Lauraceae	Lauraceae sp1	2	0.32	678.78	0.11	2	0.58	1.01
Sterculiaceae	<i>Dombeya</i> sp8	2	0.32	414.82	0.07	2	0.58	0.97
Meliaceae	<i>Malleastrum gracile</i>	2	0.32	264.31	0.04	2	0.58	0.95
Rutaceae	<i>Vepris</i> sp2	2	0.32	229.22	0.04	2	0.58	0.94
Monimiaceae	Monimiaceae sp3	2	0.32	215.39	0.04	2	0.58	0.94
Rubiaceae	Rubiaceae sp16	2	0.32	207.74	0.03	2	0.58	0.94
Rubiaceae	<i>Psychotria</i> sp6	2	0.32	197.43	0.03	2	0.58	0.93
Araliaceae	<i>Polyscias</i> sp7	1	0.16	206.12	0.03	2	0.58	0.78
Verbenaceae	<i>Clerodendrum</i> sp1	2	0.32	467.98	0.08	1	0.29	0.69
Aquifoliaceae	<i>Ilex mitis</i>	2	0.32	210.34	0.03	1	0.29	0.65
Clusiaceae	<i>Mammea</i> sp2	1	0.16	907.92	0.15	1	0.29	0.60
Rutaceae	<i>Zanthoxylum</i> sp1	1	0.16	829.58	0.14	1	0.29	0.59
Myrtaceae	Myrtaceae sp3	1	0.16	706.86	0.12	1	0.29	0.57
Euphorbiaceae	<i>Drypetes</i> sp1	1	0.16	480.87	0.08	1	0.29	0.53
Lauraceae	Lauraceae sp8	1	0.16	422.73	0.07	1	0.29	0.52
Elaeocarpaceae	<i>Elaeocarpus</i> sp3	1	0.16	390.57	0.06	1	0.29	0.52
Moraceae	<i>Ficus sorocoeoides</i>	1	0.16	260.16	0.04	1	0.29	0.49
Euphorbiaceae	<i>Croton</i> sp2	1	0.16	226.98	0.04	1	0.29	0.49
Rubiaceae	Rubiaceae sp14	1	0.16	224.32	0.04	1	0.29	0.49
Myrsinaceae	<i>Oncostemum</i> sp11	1	0.16	213.82	0.04	1	0.29	0.49
Erythroxylaceae	<i>Erythroxylum</i> sp3	1	0.16	143.14	0.02	1	0.29	0.47
Moraceae	<i>Ficus</i> sp2	1	0.16	136.83	0.02	1	0.29	0.47
Rubiaceae	<i>Pouridianta</i> sp1	1	0.16	103.87	0.02	1	0.29	0.47
Asteraceae	<i>Vernonia</i> sp1	1	0.16	83.32	0.01	1	0.29	0.46
Total		623	100.00	606,339.31	100.00	344	100.00	300.00

Plot 5 at 1875 m

Family	Genus species	Number of individuals	Relative density (%)	Basal area (cm ²)	Relative dominance (%)	Absolute frequency	Relative frequency	IVI
Araliaceae	<i>Polyscias</i> sp7	153	11.38	106,034.75	16.27	10	4.35	32.00
Clusiaceae	<i>Garcinia</i> sp2	105	7.84	27,789.75	4.26	10	4.35	16.45
Lauraceae	<i>Belschmedia</i> sp1	60	4.48	45,719.00	7.02	8	3.48	14.97
Flacourtiaceae	<i>Aphloia theaeiformis</i>	68	5.04	37,254.25	5.72	9	3.91	14.67
Elaeocarpaceae	<i>Sloanea rhodantha</i> var. <i>quercifolia</i>	40	2.99	44,111.00	6.77	7	3.04	12.80
Cunoniaceae	<i>Weinmannia</i> sp4	38	2.80	47,114.50	7.23	5	2.17	12.20
Araliaceae	<i>Polyscias</i> sp9	73	5.41	15,948.00	2.45	9	3.91	11.77
Celastraceae	<i>Brexiella</i> sp1	75	5.60	19,788.25	3.04	7	3.04	11.68
Aquifoliaceae	<i>Ilex mitis</i>	53	3.92	25,937.75	3.98	6	2.61	10.51
Lauraceae	<i>Cryptocarya</i> sp3	40	2.99	24,867.00	3.82	8	3.48	10.28
Lauraceae	Lauraceae sp16	30	2.24	25,314.50	3.88	6	2.61	8.73

Appendix 4-4 Continued.

Family	Genus species	Number of individuals	Relative density (%)	Basal area (cm ²)	Relative dominance (%)	Absolute frequency	Relative frequency	IVI
Monimiaceae	<i>Ehippiandra</i> sp1	45	3.36	11,739.00	1.80	7	3.04	8.20
Ericaceae	<i>Agauria</i> sp1	18	1.31	25,367.75	3.89	5	2.17	7.37
Cunoniaceae	<i>Weinmannia</i> sp6	20	1.49	20,531.00	3.15	5	2.17	6.82
Erythroxylaceae	<i>Erythroxylum</i> sp4	35	2.61	5,508.25	0.85	7	3.04	6.50
Rubiaceae	Rubiaceae sp1	28	2.05	8,408.75	1.29	7	3.04	6.39
Myrtaceae	Myrtaceae sp20	28	2.05	7,923.00	1.22	7	3.04	6.31
Myrsinaceae	<i>Onocostemum</i> sp12	38	2.80	5,109.50	0.78	6	2.61	6.19
Elaeocarpaceae	<i>Elaeocarpus</i> sp4	23	1.68	8,021.00	1.23	7	3.04	5.95
Elaeocarpaceae	<i>Sloanea rhodantha</i> var. <i>rhodantha</i>	13	0.93	17,880.75	2.74	5	2.17	5.85
Myrtaceae	<i>Syzygium</i> sp2	38	2.80	4,437.25	0.68	5	2.17	5.65
Verbenaceae	<i>Vitex</i> sp4	30	2.24	4,880.75	0.75	5	2.17	5.16
Rubiaceae	Rubiaceae sp17	23	1.68	4,767.75	0.73	6	2.61	5.02
Pittosporaceae	<i>Pittosporum</i> sp1	18	1.31	6,451.50	0.99	6	2.61	4.90
Myrtaceae	Myrtaceae sp22	18	1.31	6,185.00	0.95	6	2.61	4.86
Lauraceae	<i>Ocotea</i> sp3	23	1.68	8,750.25	1.34	4	1.74	4.76
Pandanaceae	<i>Pandanus</i> sp2	20	1.49	3,772.00	0.58	6	2.61	4.68
Lauraceae	Lauraceae sp1	15	1.12	10,056.75	1.54	4	1.74	4.40
Flacourtiaceae	Flacourtiaceae sp1	15	1.12	6,560.25	1.01	5	2.17	4.30
Rubiaceae	Rubiaceae sp18	15	1.12	3,101.00	0.48	5	2.17	3.77
Sterculiaceae	Sterculiaceae sp2	13	0.93	6,564.50	1.01	4	1.74	3.68
Euphorbiaceae	<i>Macaranga</i> sp2	18	1.31	3,572.75	0.55	4	1.74	3.59
Cunoniaceae	<i>Weinmannia</i> sp7	13	0.93	7,314.00	1.12	2	0.87	2.92
Lauraceae	Lauraceae sp3	8	0.56	9,306.75	1.43	2	0.87	2.86
Araliaceae	<i>Schefflera</i> sp2	8	0.56	7,635.00	1.17	2	0.87	2.60
Euphorbiaceae	<i>Croton</i> sp3	10	0.75	3,571.25	0.55	3	1.30	2.60
Myrtaceae	Myrtaceae sp18	10	0.75	1,182.25	0.18	3	1.30	2.23
Sterculiaceae	<i>Dombeya</i> sp12	15	1.12	4,283.25	0.66	1	0.43	2.21
Rutaceae	<i>Vepris</i> sp1	13	0.93	2,631.50	0.40	2	0.87	2.21
Lauraceae	Lauraceae sp6	8	0.56	4,947.00	0.76	2	0.87	2.19
Sterculiaceae	<i>Dombeya</i> sp12	5	0.37	4,532.50	0.70	1	0.43	1.50
Cyatheaceae	<i>Cyathea</i> sp1	5	0.37	956.75	0.15	2	0.87	1.39
Myrtaceae	Myrtaceae sp21	5	0.37	524.00	0.08	2	0.87	1.32
Myrtaceae	Myrtaceae sp17	5	0.37	2,417.00	0.37	1	0.43	1.18
Rubiaceae	<i>Gaertnera</i> sp5	5	0.37	1,019.00	0.16	1	0.43	0.96
Asteraceae	<i>Brachylaena ramiflora</i>	3	0.19	672.00	0.10	1	0.43	0.72
Myrtaceae	Myrtaceae sp19	3	0.19	368.50	0.06	1	0.43	0.68
Rubiaceae	<i>Psychotria</i> sp7	3	0.19	302.00	0.05	1	0.43	0.67
Euphorbiaceae	<i>Croton</i> sp2	3	0.19	282.75	0.04	1	0.43	0.66
Meliaceae	<i>Malleastrum</i> sp1	3	0.19	259.75	0.04	1	0.43	0.66
Total		1,340	100.00	651,672.75	100.00	230	100.00	300.00

Note: The data are ranked by decreasing values of IVI for each plot. The unidentified material is omitted.

Appendix 4-5 Relative Density, Relative Dominance, and Relative Specific Diversity from Transect Data Collected in Parcel 2 of the RNI d’Andohahela.

Family	Number of individuals	Relative density (%)	Basal area (cm ²)	Relative dominance (%)	Number of species	Relative species diversity (%)	FIV
Burseraceae	103	20.16	7,660.77	17.53	5	6.41	44.10
Didiereaceae	47	9.20	11,793.93	26.99	4	5.13	41.32
Euphorbiaceae	72	14.09	2,855.32	6.54	8	10.26	30.88
Anacardiaceae	19	3.72	9,912.51	22.69	2	2.56	28.97
Fabaceae	39	7.63	2,490.89	5.70	10	12.82	26.15
Ebenaceae	41	8.02	882.00	2.02	4	5.13	15.17
Hernandiaceae	38	7.44	2,369.15	5.42	1	1.28	14.14
Rubiaceae	14	2.74	278.62	0.64	6	7.69	11.07
Tiliaceae	21	4.11	267.82	0.61	4	5.13	9.85
Loganiaceae	17	3.33	650.51	1.49	3	3.85	8.66
Combretaceae	8	1.57	735.92	1.68	3	3.85	7.10
Boraginaceae	7	1.37	235.62	0.54	4	5.13	7.04
Apocynaceae	11	2.15	937.18	2.14	2	2.56	6.86
Bignoniaceae	15	2.94	402.71	0.92	2	2.56	6.42
Flacourtiaceae	9	1.76	138.82	0.32	3	3.85	5.93
Lythraceae	16	3.13	371.89	0.85	1	1.28	5.26
Capparidaceae	8	1.57	1,004.52	2.30	1	1.28	5.15
Urticaceae	3	0.59	84.04	0.19	3	3.85	4.63
Verbenaceae	2	0.39	208.13	0.48	2	2.56	3.43
Rutaceae	3	0.59	75.40	0.17	2	2.56	3.32
Ptaeroxylaceae	6	1.17	140.59	0.32	1	1.28	2.78
Sterculiaceae	5	0.98	77.95	0.18	1	1.28	2.44
Meliaceae	2	0.39	40.84	0.09	1	1.28	1.77
Celastraceae	1	0.20	38.48	0.09	1	1.28	1.57
Erythroxylaceae	1	0.20	19.63	0.04	1	1.28	1.52
Asclepiadaceae	1	0.20	7.07	0.02	1	1.28	1.49
Malvaceae	1	0.20	7.07	0.02	1	1.28	1.49
Cucurbitaceae	1	0.20	4.91	0.01	1	1.28	1.49
Total	511	100.00	43,692.29	100.00	78	100.00	300.00

Note: The unidentified material is omitted.

Appendix 4-6 Relative Density, Relative Dominance, and Relative Frequency from Transect Data Collected in Parcel 2 of the RNI d'Andohahela.

Family	Genus species	Number of individuals	Relative density (%)	Basal area (cm²)	Relative dominance (%)	Absolute frequency	Relative frequency	IVI
Anacardiaceae	<i>Operculicarya decaryi</i>	13	2.54	9,815.12	22.46	8	3.94	28.95
Didiereaceae	<i>Alluaudia procera</i>	29	5.68	6,415.13	14.68	8	3.94	24.30
Burseraceae	<i>Commiphora humberti</i>	37	7.24	3,014.36	6.90	9	4.43	18.57
Didiereaceae	<i>Alluaudia ascendens</i>	13	2.54	5,317.15	12.17	5	2.46	17.18
Hernandiaceae	<i>Gyrocarpus americanus</i>	38	7.44	2,369.15	5.42	6	2.96	15.81
Burseraceae	<i>Commiphora aprevalii</i>	22	4.31	2,286.29	5.23	9	4.43	13.97
Ebenaceae	<i>Diospyros humbertiana</i>	34	6.65	727.67	1.67	7	3.45	11.77
Burseraceae	<i>Commiphora marchandii</i>	17	3.33	1,465.95	3.36	8	33.94	10.62
Euphorbiaceae	<i>Euphorbia omeoclada</i>	18	3.52	696.45	1.59	7	3.45	8.56
Burseraceae	<i>Commiphora brevicalyx</i>	18	3.52	541.53	1.24	7	3.45	8.21
Fabaceae	<i>Dichrostachys</i> sp1	18	3.52	188.69	0.43	6	2.96	6.91
Euphorbiaceae	<i>Euphorbia intisy</i>	21	4.11	541.34	1.24	2	0.99	6.33
Euphorbiaceae	<i>Euphorbia plagiantha</i>	10	1.96	992.74	2.27	4	1.97	6.20
Lythraceae	Lythraceae sp1	16	3.13	371.89	0.85	4	1.97	5.95
Fabaceae	<i>Tetrapterocarpon geayi</i>	5	0.98	1,807.20	4.14	1	0.49	5.61
Burseraceae	<i>Commiphora simplicifolia</i>	9	1.76	352.64	0.81	6	2.96	5.52
Capparidaceae	<i>Boscia longifolia</i>	8	1.57	1,004.52	2.30	3	1.48	5.34
Euphorbiaceae	<i>Croton</i> sp2	15	2.94	231.10	0.53	3	1.48	4.94
Tiliaceae	<i>Grewia</i> sp2	12	2.35	166.11	0.38	4	1.97	4.70
Loganiaceae	<i>Strychnos madagascariensis</i>	13	2.54	140.59	0.32	3	1.48	4.34
Apocynaceae	<i>Pachypodium geayi</i>	5	0.98	857.65	1.96	2	0.99	3.93
Tiliaceae	<i>Grewia</i> sp1	5	0.98	64.60	0.15	5	2.46	3.59
Rubiaceae	Rubiaceae sp2	7	1.37	103.87	0.24	4	1.97	3.58
Bignoniaceae	<i>Fernandoa madagascariensis</i>	7	1.37	290.99	0.67	3	1.48	3.51
Bignoniaceae	<i>Stereospermum nematocarpus</i>	8	1.57	111.72	0.26	3	1.48	3.30
Ptaeroxylaceae	<i>Cedrelopsis grevei</i>	6	1.17	140.59	0.32	3	1.48	2.97
Flacourtiaceae	Flacourtiaceae sp1	6	1.17	100.73	0.23	3	1.48	2.88
Combretaceae	<i>Terminalia monoceros</i>	1	0.20	380.13	0.87	3	1.48	2.54
Fabaceae	Fabaceae sp1	7	1.37	293.15	0.67	1	0.49	2.53
Anacardiaceae	<i>Rhus perrieri</i>	6	1.17	97.39	0.22	2	0.99	2.38
Apocynaceae	Apocynaceae sp1	6	1.17	79.52	0.18	2	0.99	2.34
Rubiaceae	Rubiaceae sp1	3	0.59	71.67	0.16	3	1.48	2.23
Fabaceae	<i>Cassia</i> sp1	3	0.59	65.19	0.15	3	1.48	2.21
Combretaceae	<i>Terminalia</i> sp2	4	0.78	115.45	0.26	2	0.99	2.03
Didiereaceae	<i>Alluaudia dumosa</i>	4	0.78	56.75	0.13	2	0.99	1.90
Loganiaceae	<i>Strychnos</i> sp2	1	0.20	490.87	1.12	1	0.49	1.81
Euphorbiaceae	<i>Euphorbia stenoclada</i>	3	0.59	277.25	0.63	1	0.49	1.71
Sterculiaceae	Sterculiaceae sp1	5	0.98	77.95	0.18	1	0.49	1.65
Tiliaceae	<i>Grewia</i> sp3	3	0.59	30.04	0.07	2	0.99	1.64
Combretaceae	<i>Terminalia</i> sp1	3	0.59	240.33	0.55	1	0.49	1.63

Appendix 4-6 Continued.

Family	Genus species	Number of individuals	Relative density (%)	Basal area (cm ²)	Relative dominance (%)	Absolute frequency	Relative frequency	IVI
Euphorbiaceae	<i>Euphorbia lecodendron</i>	2	0.39	91.89	0.21	2	0.99	1.59
Ebenaceae	<i>Diospyros</i> sp1	2	0.39	91.11	0.21	2	0.99	1.59
Rutaceae	<i>Zanthoxylum decaryi</i>	2	0.39	62.83	0.14	2	0.99	1.52
Meliaceae	<i>Neobeguea mahafaliensis</i>	2	0.39	40.84	0.09	2	0.99	1.47
Flacourtiaceae	Flacourtiaceae sp2	2	0.39	33.18	0.08	2	0.99	1.45
Verbenaceae	Verbenaceae sp2	1	0.20	113.10	0.26	2	0.99	1.44
Boraginaceae	Boraginaceae sp1	3	0.59	145.30	0.33	1	0.49	1.41
Urticaceae	Urticaceae sp1	1	0.20	38.48	0.09	2	0.99	1.27
Fabaceae	Fabaceae sp6	1	0.20	28.27	0.06	2	0.99	1.25
Ebenaceae	<i>Diospyros quartzitarum</i>	3	0.59	45.75	0.10	1	0.49	1.18
Loganiaceae	<i>Strychnos</i> sp1	3	0.59	19.05	0.04	1	0.49	1.12
Boraginaceae	Boraginaceae sp2	2	0.39	58.12	0.13	1	0.49	1.02
Euphorbiaceae	<i>Croton</i> sp1	2	0.39	19.63	0.04	1	0.49	0.93
Ebenaceae	<i>Diospyros</i> sp2	2	0.39	17.48	0.04	1	0.49	0.92
Verbenaceae	Verbenaceae sp1	1	0.20	95.03	0.22	1	0.49	0.91
Rubiaceae	<i>Adina microcephala</i>	1	0.20	50.27	0.12	1	0.49	0.80
Celastraceae	Celastraceae sp1	1	0.20	38.48	0.09	1	0.49	0.78
Urticaceae	<i>Obetia</i> sp2	1	0.20	38.48	0.09	1	0.49	0.78
Fabaceae	Fabaceae sp2	1	0.20	28.27	0.06	1	0.49	0.75
Fabaceae	Fabaceae sp5	1	0.20	28.27	0.06	1	0.49	0.75
Rubiaceae	Rubiaceae sp4	1	0.20	28.27	0.06	1	0.49	0.75
Boraginaceae	<i>Ehretia</i> sp1	1	0.20	19.63	0.04	1	0.49	0.73
Erythroxylaceae	<i>Erythroxylum pervillei</i>	1	0.20	19.63	0.04	1	0.49	0.73
Fabaceae	<i>Bauhinia hildebrandti</i>	1	0.20	19.63	0.04	1	0.49	0.73
Fabaceae	Fabaceae sp3	1	0.20	19.63	0.04	1	0.49	0.73
Rubiaceae	Rubiaceae sp3	1	0.20	19.63	0.04	1	0.49	0.73
Boraginaceae	<i>Ehretia</i> sp2	1	0.20	12.57	0.03	1	0.49	0.72
Fabaceae	Fabaceae sp4	1	0.20	12.57	0.03	1	0.49	0.72
Rutaceae	Rutaceae sp1	1	0.20	12.57	0.03	1	0.49	0.72
Asclepiadaceae	<i>Cyanthum</i> sp1	1	0.20	7.07	0.02	1	0.49	0.70
Malvaceae	Malvaceae sp1	1	0.20	7.07	0.02	1	0.49	0.70
Tiliaceae	<i>Grewia</i> sp4	1	0.20	7.07	0.02	1	0.49	0.70
Urticaceae	<i>Obetia</i> sp1	1	0.20	7.07	0.02	1	0.49	0.70
Cucurbitaceae	Cucurbitaceae sp1	1	0.20	4.91	0.01	1	0.49	0.70
Didieraceae	<i>Alluaudia humbertii</i>	1	0.20	4.91	0.01	1	0.49	0.70
Euphorbiaceae	<i>Croton</i> sp3	1	0.20	4.91	0.01	1	0.49	0.70
Flacourtiaceae	<i>Flacourtia</i> sp1	1	0.20	4.91	0.01	1	0.49	0.70
Rubiaceae	Rubiaceae sp5	1	0.20	4.91	0.01	1	0.49	0.70
Total		511	100.00	43,692.29	100.00	203	100.00	300.00

Note: The unidentified material is omitted.

Chapter 5

A Regional Analysis of Species Associations and Distributions of Two Caddisfly Families (Trichoptera: Hydropsychidae and Philopotamidae) in Southeastern Madagascar

François-Marie Gibon¹ and Patricia Zoé Andriambelo¹

Abstract

Specimens of the caddisfly (Trichoptera) families Hydropsychidae and Philopotamidae collected in the Réserve Naturelle Intégrale d'Andohahela and surrounding areas are discussed and identified. An examination of the regional distribution of these caddisflies at the species level using correspondence analysis clearly shows a distinct faunal separation between the humid eastern forests and dry western forest habitats.

Résumé

Des récoltes de Trichoptères Hydropsychidae and Philopotamidae, déterminées au niveau de l'espèce, ont été menées au sein de la Réserve Naturelle Intégrale d'Andohahela et à sa périphérie. Le traitement des données au moyen de l'analyse des correspondances met en évidence une nette séparation entre les faunes de l'habitat humide de l'Est et celle colonisant la zone aride de l'Ouest.

Introduction

For the past 6 years a project entitled "Biotypologie et biodiversité des eaux continentales malgaches," jointly run by ORSTOM (Institut Français de Recherche pour le Développement en Coopération) and CNRE (Centre National de Recherche sur l'Environnement), has been actively studying the freshwater faunas of Madagascar. The aim of this work is to understand certain aspects of freshwater organisms living in the river and stream systems of the island, including taxonomy, ecology, distribution, and biotic and abiotic aspects that are related to their biogeography. Taxa that appear to be good indicators of certain

environmental conditions and are easy to collect were chosen for detailed studies. Among these are Trichoptera (Annulipalpia) belonging to the two families Hydropsychidae and Philopotamidae. We have now obtained sufficient collections and distributional information from southeastern Madagascar, including the Réserve Naturelle Intégrale (RNI) d'Andohahela, to present a synthesis of our results. The geographical area is defined by the hydrological basins of the Mandrare, Efaho, Manampanihy, and all small rivers between the Mandrare to the west and the Manampanihy to the north.

Our analysis emphasizes faunistic associations and linked ecological parameters. One of the main factors that we underline is the role of the eastern primary humid forests of the region, particularly the RNI d'Andohahela and surrounding areas.

¹ ORSTOM, BP 434, Antananarivo (101), Madagascar.

Methods

Sites were chosen in order to include the major climatic zones of the region (western and eastern; see Chapters 1 and 2) and the different stream orders. We also tried to work at different altitudes and in different vegetational zones (or soil occupations). Logistic and climatic conditions have sometimes considerably influenced our choice of sites. To date 56 sites have been sampled at least once in southeastern Madagascar. Although the database is by no means complete, it is sufficient to obtain a broad perspective and detect important ecological parameters associated with the distribution of these trichopterans.

The study of Trichoptera at the species level is only possible with adults (especially males, because most females cannot be specifically identified). Generally these insects are captured using a system of light traps of two types—gas and black light. Nets are also used. General trapping methods are described in more detail by Gibon et al. (1994, 1996). Samples are preserved in alcohol (70%).

We have been working on an almost unknown fauna (Gibon & Elouard, 1996), and much of our ecological work depends first on working out the alpha-taxonomical aspects of these organisms. There are two main collections of Malagasy caddisflies. The first is the Institut de Recherche Scientifique de Madagascar (IRSM) collection deposited at the Muséum National d'Histoire Naturelle (MNHN), Paris. J. Oláh (Czarvas, Hungary) is currently working on this first collection, which contains more than 220 species. He has shared his results, allowing us to coordinate taxonomic studies. The second collection is at the Laboratoire de Recherche sur les Systèmes Aquatiques et leur Environnement (LRSAE), Antananarivo, and contains more than 500 species. The morphology of the male genitalia of all species is studied in detail. This technique, which is basically a morpho-species approach, allows us to complete ecological analyses before Latin binomials are available for many of these organisms and in turn to transfer data to conservation managers without having to wait for long-term taxonomic publications.

Information has been installed into the "Bibi-soa" database, written at the LRSAE with NOE software (Hertu & Elouard, 1997). Cartography is realized by CartoNOE software (Hertu, 1995). Data were treated by correspondence analysis (CA) (Gauch, 1992) with ADE software written by Chessel and Dolédec.

Results

The following list contains the sites that have been sampled and used in the analysis presented below. For each station (= St) information is given on (1) the code number of the drainage basin (12 = Mandrare, 41 = Manampanihy, 89 = Efa-ho, 108 = Tarantsy, and 109 = small coastal basins of Manantenina); (2) the name of the nearest locality (when available); (3) the elevation (meters above sea level [masl]); (4) the longitude; (5) the latitude; and (6) names of captured genera and species or morphospecies (Table 5-1).

Sampled Sites

- St12-01—Andratina at Imanombo, 213 m, 45°57'32"E, 24°20'20"S. *Cheumatopsyche* sp. AH; *Macrostemum adpictum*, *Macrostemum scriptum*; *Chimarra* spp. AH, AI, *Chimarra dybowskina*.
- St12-03—Mandrare at Anadabolava, 209 m, 46°18'30"E, 24°13'18"S. *Cheumatopsyche* spp. AH, AI, A, L; *Macrostemum adpictum*, *Macrostemum scriptum*, *Macrostemum* spp. C, K; *Potamyia* sp. F; *Chimarra* spp. E, AH, AI, A, C, Y.
- St12-04—Unnamed small tributary at Amboanemba, 223 m, 46°27'45"E, 24°40'33"S. *Cheumatopsyche* sp. AH; *Macrostemum adpictum*; *Chimarra* spp. AH, AI.
- St12-06—Mandrare at Ifotaka, 60 m, 46°08'14"E, 24°47'55"S. *Cheumatopsyche* sp. AH.
- St12-07—Unnamed small tributary at Berenty, 20 m, 46°18'14"E, 24°59'37"S. *Chimarra* sp. AH.
- St12-08—Sambalaly at Talakifeno, 145 m, 46°40'59"E, 24°49'55"S. *Macrostemum adpictum*, *Macrostemum scriptum*; *Chimarra* sp. AH.
- St12-09—Imonty at Imonty, 175 m, 46°41'27"E, 24°48'51"S. *Cheumatopsyche* sp. C; *Macrostemum adpictum*; *Chimarra dybowskina*.
- St12-10—Mananara at Betanimena, 118 m, 46°39'20"E, 24°48'17"S. *Macrostemum adpictum*, *Macrostemum scriptum*; *Chimarra* spp. AH, AI, D, O.
- St12-12—Imonty at Imonty, 500 m, 46°43'18"E, 24°49'03"S. *Chimarra* spp. AH, I, AF, AU, AG; *Paulianodes* sp. A.
- St12-14—Sahandrojo at Betenina, 325 m, 46°25'25"E, 24°25'12"S. *Cheumatopsyche* sp.

TABLE 5-1. Taxonomic status of Trichoptera (Hydropsychidae and Philopotamidae) known from southeastern Madagascar

Species	Taxonomic status	Bibliography
<i>Cheumatopsyche</i> sp. A	LRSAE (in prep.)	1
<i>Cheumatopsyche</i> sp. AH	Olàh/LRSAE (in prep.)	1
<i>Cheumatopsyche</i> sp. AI	Olàh/LRSAE (in prep.)	1
<i>Cheumatopsyche</i> sp. AK	Olàh/LRSAE (in prep.)	
<i>Cheumatopsyche</i> sp. AF	LRSAE (in prep.)	
<i>Cheumatopsyche</i> sp. C	LRSAE (in prep.)	
<i>Cheumatopsyche</i> sp. L	LRSAE (in prep.)	
<i>Hydropsyche</i> sp. A	LRSAE (in prep.)	
<i>Leptonema conicum</i>	Flint et al. (1987)	4
<i>Leptonema milae</i>	Sykora (1964)	4
<i>Leptonema madagascariense</i>	Ulmer (1905)	4
<i>Leptonema</i> sp. E	LRSAE (in prep.)	
<i>Leptonema</i> sp. G	LRSAE (in prep.)	
<i>Macrostemum adpictum</i>	Navàs (1935)	
<i>Macrostemum placidum</i>	Navàs (1935)	
<i>Macrostemum scriptum</i>	Rambur (1842)	1
<i>Macrostemum</i> sp. C	LRSAE (in prep.)	
<i>Macrostemum</i> sp. D	LRSAE (in prep.)	
<i>Macrostemum</i> sp. K	LRSAE (in prep.)	
<i>Macrostemum</i> sp. O	LRSAE (in prep.)	
<i>Polymorphanisus guttatus</i>	Navàs (1935)	5
<i>Potamyia</i> sp. E	Olàh/LRSAE (in prep.)	
<i>Potamyia</i> sp. F	Olàh/LRSAE (in prep.)	
<i>Chimarra</i> sp. A	LRSAE (in prep.)	1, 3
<i>Chimarra</i> sp. B	LRSAE (in prep.)	1
<i>Chimarra</i> sp. D	LRSAE (in prep.)	2
<i>Chimarra</i> sp. E	Olàh/LRSAE (in prep.)	2
<i>Chimarra</i> sp. F	LRSAE (in prep.)	
<i>Chimarra</i> sp. G	LRSAE (in prep.)	
<i>Chimarra</i> sp. I	Olàh/LRSAE (in prep.)	2, 3
<i>Chimarra</i> sp. O	LRSAE (in prep.)	3
<i>Chimarra</i> sp. Y	LRSAE (in prep.)	
<i>Chimarra</i> sp. AE	Olàh/LRSAE (in prep.)	2
<i>Chimarra</i> sp. AF	Olàh/LRSAE (in prep.)	2
<i>Chimarra</i> sp. AG	Olàh/LRSAE (in prep.)	2
<i>Chimarra</i> sp. AH	Olàh/LRSAE (in prep.)	1, 2, 3
<i>Chimarra</i> sp. AI	Olàh/LRSAE (in prep.)	3
<i>Chimarra</i> sp. AK	Olàh/LRSAE (in prep.)	1, 3
<i>Chimarra</i> sp. AN	LRSAE (in prep.)	
<i>Chimarra</i> sp. AP	LRSAE (in prep.)	
<i>Chimarra</i> sp. AQ	LRSAE (in prep.)	
<i>Chimarra</i> sp. AS	Olàh/LRSAE (in prep.)	
<i>Chimarra</i> sp. AT	LRSAE (in prep.)	
<i>Chimarra</i> sp. AU	Olàh/LRSAE (in prep.)	
<i>Chimarra</i> sp. AV	Olàh/LRSAE (in prep.)	
<i>Chimarra dybowskina</i>	Navàs (1931)	1, 3
<i>Dolophilodes</i> sp. C	LRSAE (in prep.)	
<i>Paulianodes</i> sp. A	LRSAE (in prep.)	
<i>Paulianodes</i> sp. F	LRSAE (in prep.)	
<i>Paulianodes</i> sp. K	LRSAE (in prep.)	
<i>Wormaldia</i> sp. D	LRSAE (in prep.)	

Key to references: 1, Elouard et al. (1994); 2, Gibon et al. (1996); 3, Gibon and Elouard (1996); 4, Flint et al. (1987); and 5, Barnard (1980).

- AH; *Macrostemum adpictum*; *Chimarra* spp. AH, AI.
- St12-15—Bezavo at Iloty, 525 m, 46°36'32"E, 24°38'10"S. *Cheumatopsyche* spp. AH, A, C; *Macrostemum adpictum*; *Chimarra* spp. AS, AH, AI.
- St12-16—Marotoko upstream of Hazofotsy, 98 m, 46°35'46"E, 24°48'47"S. *Cheumatopsyche* sp. AH, C; *Macrostemum adpictum*; *Chimarra* sp. AH.
- St12-17—Mananara at Hazofotsy, 98 m, 46°35'46"E, 24°48'57"S. *Cheumatopsyche* sp. C; *Macrostemum adpictum*; *Chimarra* sp. AH.
- St12-19—Mananara-Sud near Amboasary, 46 m, 46°26'34"E, 24°51'03"S. *Cheumatopsyche* sp. AH; *Macrostemum adpictum*.
- St12-20—Marotoko, 2 km north of Mananara, 275 m, 46°38'50"E, 24°44'02"S. *Cheumatopsyche* spp. AH, C; *Macrostemum adpictum*, *Macrostemum scriptum*; *Chimarra* spp. AH, AI.
- St12-21—Tributary of Mananara at Amboanemba, 223 m, 46°27'45"E, 24°40'40"S. *Cheumatopsyche* sp. AH; *Macrostemum adpictum*; *Chimarra* spp. AH, AI.
- St12-22—Manambolo at 7 km north of Berohanga, 440 m, 46°35'11"E, 24°35'07"S. *Cheumatopsyche* sp. AH; *Macrostemum adpictum*, *Macrostemum scriptum*; *Chimarra* spp. AS, AH, AI.
- St12-23—Bezavo at Berohanga near Lotibe, 550 m, 46°36'07"E, 24°38'57"S. *Cheumatopsyche* spp. AH, A; *Macrostemum adpictum*, *Macrostemum scriptum*; *Chimarra* spp. AS, AH, AI, AK.
- St12-25—Small tributary of Mandrare between Tranomaro and Tsivory, 280 m, 46°24'25"E, 24°24'27"S. *Cheumatopsyche* sp. AH; *Macrostemum adpictum*; *Chimarra* spp. AH, AI.
- St12-26—Small unnamed tributary at Tsivory, 324 m, 46°00'21"E, 24°06'43"S. *Cheumatopsyche* sp. AH; *Macrostemum adpictum*, *Macrostemum scriptum*; *Chimarra* sp. AH.
- St12-27—Sakamamba at Imanombo, 340 m, 45°45'59"E, 24°28'32"S. *Cheumatopsyche* sp. AH; *Macrostemum adpictum*, *Macrostemum scriptum*; *Chimarra* spp. AH, AI, *Chimarra dybowskina*.
- St12-29—Antalimanga at Besomosoy, 272 m, 46°27'59"E, 24°05'45"S. *Cheumatopsyche* spp. AH, AI, A; *Macrostemum adpictum*; *Chimarra* spp. AH, AI.
- St12-30—Small unnamed tributary near Andaza, 315 m, 46°34'05"E, 24°03'16"S. *Cheumatopsyche* spp. AH, AI, A; *Macrostemum adpictum*, *Macrostemum scriptum*; *Potamyia* sp. F; *Chimarra* spp. AH, AI.
- St12-31—Tributary of Sohitay at Ankazomanga, 430 m, 46°37'23"E, 24°02'37"S. *Cheumatopsyche* spp. AH, A, C; *Macrostemum adpictum*, *Macrostemum scriptum*; *Potamyia* sp. F; *Chimarra* spp. AH, B, O.
- St12-33—Manambolo tributary of Mandrare at Maromby, 345 m, 46°34'39"E, 24°23'36"S. *Cheumatopsyche* sp. AH; *Macrostemum adpictum*; *Potamyia* sp. F; *Chimarra* spp. AH, AI.
- St12-34—Abetolo tributary at Esira, 400 m, 46°41'07"E, 24°18'00"S. *Cheumatopsyche* sp. AH; *Macrostemum adpictum*; *Chimarra* spp. AH, AI.
- St12-35—Anatranatra between Esira and Maroasara, 325 m, 46°39'04"E, 24°17'37"S. *Cheumatopsyche* sp. AH; *Macrostemum adpictum*; *Potamyia* sp. F; *Chimarra* spp. AH, AI, O.
- St12-36—Betroky at Tranomaro, 260 m, 46°28'30"E, 24°35'47"S. *Cheumatopsyche* sp. AH; *Macrostemum adpictum*; *Chimarra* sp. AH.
- St12-37—Esomony at Esomony, 475 m, 46°37'28"E, 24°30'53"S. *Cheumatopsyche* sp. AH; *Macrostemum adpictum*; *Chimarra* sp. AH, *Chimarra dybowskina*.
- St12-38—Sakamalio in the RNI d'Andohahela, 750 m, 46°40'56"E, 24°32'07"S. *Cheumatopsyche* spp. AH, A, AF, C; *Leptonema conicum*, *Leptonema* sp. G; *Macrostemum scriptum*; *Potamyia* sp. E; *Chimarra* spp. AS, I, AV, *Chimarra dybowskina*, *Chimarra* sp. AU.
- St12-39—Sakamalio in the RNI d'Andohahela, 725 m, 46°40'49"E, 24°32'13"S. *Cheumatopsyche* sp. A; *Macrostemum adpictum*, *Macrostemum scriptum*; *Potamyia* sp. E; *Chimarra* sp. I, *Chimarra dybowskina*, *Chimarra* sp. AU.
- St41-01—Tributary of Manampanihy at Fenoovo, 72 m, 46°53'39"E, 24°41'00"S. *Macrostemum scriptum*; *Chimarra* spp. AS, AV, AK, *Chimarra dybowskina*, *Chimarra* spp. AF, A, F, G; *Paulianodes* sp. A.
- St41-05—Manampanihy at Manantenina (ferry crossing), 2 m, 47°18'57"E, 24°16'08"S. *Macrostemum scriptum*; *Chimarra* spp. AK, A.
- St41-06—Manampanihy at Enosiary, 98 m, 46°49'19"E, 24°40'37"S. *Cheumatopsyche* sp. A; *Macrostemum placidum*, *Macrostemum*

scriptum, *Macrostemum* sp. D; *Potamyia* sp. E; *Chimarra* spp. AH, AN, AQ.

St41-07—Andranohela at Bevoay, 98 m, 46°49'25"E, 24°40'00"S. *Cheumatopsyche* sp. A; *Macrostemum placidum*, *Macrostemum scriptum*; *Potamyia* sp. E; *Chimarra dybowskina*, *Chimarra* spp. AN, AQ.

St41-09—Andranohela at camp 1 in the RNI d'Andohahela, 440 m, 46°45'34"E, 24°36'43"S. *Cheumatopsyche* sp. L; *Hydropsyche* sp. A; *Leptonema milae*; *Macrostemum* sp. O; *Polymorphanisus guttatus*; *Chimarra* spp. AH, AP, AG; *Paulianodes* sp. F.

St41-12—Andranohela at camp 2 in the RNI d'Andohahela, 810 m, 46°44'25"E, 24°35'47"S. *Leptonema milae*; *Macrostemum* sp. O; *Paulianodes* sp. A.

St41-13—Tributary of Andranohela at camp 2 in the RNI d'Andohahela, ~810 m, 46°44'09"E, 24°35'40"S. *Leptonema* sp. E; *Macrostemum* sp. O.

St41-15—Andranohela at camp 2 in the RNI d'Andohahela ~810 m, 46°44'19"E, 24°35'33"S. *Leptonema milae*; *Macrostemum* sp. O; *Chimarra* sp. F.

St89-01—Efaho at Ifarantsa, 20 m, 46°52'12"E, 24°55'37"S. *Cheumatopsyche* spp. A, C; *Macrostemum adpictum*, *Macrostemum placidum*, *Macrostemum scriptum*; *Chimarra* spp. AH, AT.

St89-02—Efaho at Soanierana, 20 m, 46°52'07"E, 24°48'20"S. *Cheumatopsyche* sp. A; *Macrostemum adpictum*, *Macrostemum scriptum*.

St89-03—Small unnamed tributary at Ranopiso I Ambany, 45 m, 46°40'23"E, 25°02'13"S. *Cheumatopsyche* sp. AH; *Macrostemum scriptum*; *Chimarra* sp. AH, *Chimarra dybowskina*, *Chimarra* spp. B, O.

St89-04—Ambahibe at Isaka-Ivondro, 50 m, 46°51'46"E, 24°47'03"S. *Macrostemum scriptum*; *Chimarra* sp. AV, *Chimarra dybowskina*, *Chimarra* sp. A.

St89-05—Ambahibe at Isaka-Ivondro, 70 m, 46°51'53"E, 24°46'47"S. *Cheumatopsyche* sp. AF; *Leptonema conicum*; *Macrostemum placidum*, *Macrostemum scriptum*; *Potamyia* sp. E; *Chimarra* spp. AH, A, *Chimarra dybowskina*, *Chimarra* sp. O.

St89-06—Ambahibe in the RNI d'Andohahela, 330 m, 46°51'09"E, 24°45'07"S. *Cheumatopsyche* sp. AK; *Dolophilodes* sp. C; *Paulianodes* spp. A, F; *Wormaldia* sp. D.

St89-07—Ambahibe in the RNI d'Andohahela,

100 m, 46°51'39"E, 24°46'23"S. *Paulianodes* sp. F.

St89-08—Ambahibe at Ezoambo, 25 m, 46°51'59"E, 24°49'10"S. *Cheumatopsyche* sp. A; *Macrostemum adpictum*, *Macrostemum placidum*, *Macrostemum scriptum*.

St89-09—Small unnamed tributary at Manambaro, 20 m, 46°49'35"E, 25°01'27"S. *Macrostemum adpictum*, *Macrostemum scriptum*; *Chimarra* sp. AH.

St89-10—Antsanira at Ranopiso II Ambony, 100 m, 46°39'30"E, 25°01'27"S. *Macrostemum scriptum*; *Chimarra dybowskina*.

St89-11—Ambahibe in the RNI d'Andohahela, 200 m, 46°51'07"E, 24°46'17"S. *Paulianodes* spp. F, K.

St89-12—Small unnamed tributary at Soanierana, 20 m, 46°52'28"E, 25°00'10"S. *Chimarra* sp. AH.

St89-13—Small unnamed tributary, 120 m, 46°52'11"E, 24°46'38"S. *Macrostemum adpictum*, *Macrostemum placidum*, *Macrostemum scriptum*; *Potamyia* sp. E; *Chimarra* sp. AH, AV, AK, *Chimarra dybowskina*, *Chimarra* sp. O.

St108-01—Tarantsy at Bevilany, 75 m, 46°35'28"E, 25°00'13"S. *Chimarra* spp. AH, A.

St108-04—Tarantsy at Antsovela, 20 m, 46°28'12"E, 25°04'47"S. *Chimarra* sp. AH.

St109-02—Antorendrika at Belavenoka, 20 m, 47°05'02"E, 24°50'18"S. *Chimarra* sp. C.

St109-04—Anandrano, 12 m, 46°58'53"E, 24°56'43"S. *Chimarra* sp. A.

Information on the stream ecology of each site is presented in Table 5-2. As usual in studies associated with the distribution of organisms on Madagascar, the first major separation of Trichoptera groups falls out according to eastern (humid) and western (dry) habitats. For this reason subsequent analyses have been conducted separately for each habitat type, and also the two trichopteran families have been separated. Four factorial diagrams are presented corresponding to: (1) Hydropsychidae species of the Mandrare and Tarantsy basins plotted according to the 1st and 2nd axes (Fig. 5-1); (2) Philopotamidae species of the Mandrare and Tarantsy basins plotted according to the 1st and 2nd axes (Fig. 5-2); (3) Hydropsychidae species of the eastern basins plotted according to the 3rd and 4th axes (the 1st and 2nd axes isolate, respectively, *Leptonema madagascariense* and *Cheumatopsyche* sp. AK, both of

TABLE 5-2. Various parameters associated with each station sampled.

Station	Altitude (m)	Distance* (km)	Width (m)	Water temperature (°C)	Gallery forest†	Habitat around station
St108-01	75	17	60	20	—	spiny forest
St108-04	20	36	6	25	—	spiny forest
St12-01	213	48	20	21	—	wooded savannah
St12-03	209	110	50	30	—	wooded savannah
St12-04	223	4	0.2	22	—	spiny forest
St12-06	60	210	200	22	—	spiny forest
St12-07	20	235	250	23	—	spiny forest
St12-08	145	8	3	19	—	xerophilous forest
St12-09	175	8.5	10	19	—	steppe
St12-10	118	16	12	19	+	spiny forest
St12-12	500	1	5	17	+	xerophilous forest
St12-14	325	1	1.8	20	—	steppe
St12-15	525	7.5	1.5	20	—	spiny forest
St12-16	98	23	4	19	—	spiny forest
St12-17	98	24.5	6	18	—	spiny forest
St12-19	46	41.5	8	22	—	spiny forest
St12-20	275	11	5	16	—	xerophilous forest
St12-21	223	32	4	16	—	spiny forest
St12-22	440	19	3	16	+	grassland
St12-23	550	6	2	18	+	grassland
St12-25	280	13	0.5	19	—	steppe
St12-26	324	9.5	1	21	—	grassland
St12-27	340	18.5	3	24	—	wooded savannah
St12-29	272	11	0.3	27	—	steppe
St12-30	315	13	12	25	—	steppe
St12-31	430	2	0.1	25	+	steppe
St12-33	345	50	7	25	—	wooded savannah
St12-34	400	9	0.1	27	+	steppe
St12-35	325	21.5	0.4	25	+	steppe
St12-36	260	19	15	24	—	grassland
St12-37	475	3	1	24	+	spiny forest
St12-38	750	3	1	22	+	grassland
St12-39	725	8	12	21	+	grassland
St41-01	72	10.5	5	21	—	grassland
St41-05	2	90	400	25	—	grassland
St41-06	98	18	35	19.5	—	grassland
St41-07	98	17	15	23	—	grassland
St41-09	525	5	15	21	+	primary humid forest
St41-12	850	4.5	10	17	+	primary humid forest
St41-13	925	3.5	4	18	+	primary humid forest
St41-15	900	4	5	18	+	primary humid forest
St89-01	20	27	20	26	—	steppe
St89-02	20	38	200	20	+	spiny bush
St89-03	45	4	2.5	20	+	steppe
St89-04	50	6.5	7	20	+	secondary humid forest
St89-05	70	3.5	5	26	+	secondary humid forest
St89-06	330	3	6.5	16	+	secondary humid forest
St89-07	100	5	4.5	19	+	secondary humid forest
St89-08	25	11	10	20	—	spiny bush
St89-09	20	16	50	17	—	spiny bush
St89-10	100	2	2	20	—	grassland
St89-11	200	1	11.5	16.5	+	secondary humid forest
St89-12	20	33.5	110	17	—	spiny bush
St89-13	120	3	4	24	+	secondary humid forest
St109-02	20	12.5	40	23	—	wooded savannah
St109-04	12	3	10	23.5	—	grassland

See text for explanation of station acronyms.

* Distance refers to estimated or measured distance of sampling site from sources.

† Gallery forest refers to the presence (+) or absence (—) of forest along the banks of the river or stream in the vicinity of the sampling station.

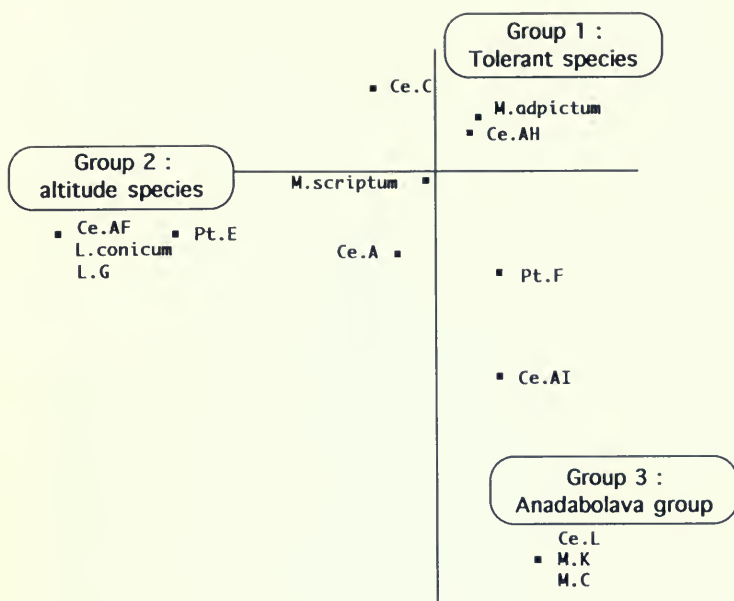


FIG. 5-1. Hydropsychidae species of the Mandrare and Tarantzy basins plotted according to the first and second axes of correspondence analysis. Generic codes: Ce. = *Cheumatopsyche*, H. = *Hydropsyche*, Pt. = *Potamyia*, M. = *Macrostemum*, L. = *Leptonema*, Po. = *Polymorphanisus*, Ci. = *Chimarra*, W. = *Wormaldia*, D. = *Dolophilodes*, and Pl. = *Paulianodes*.

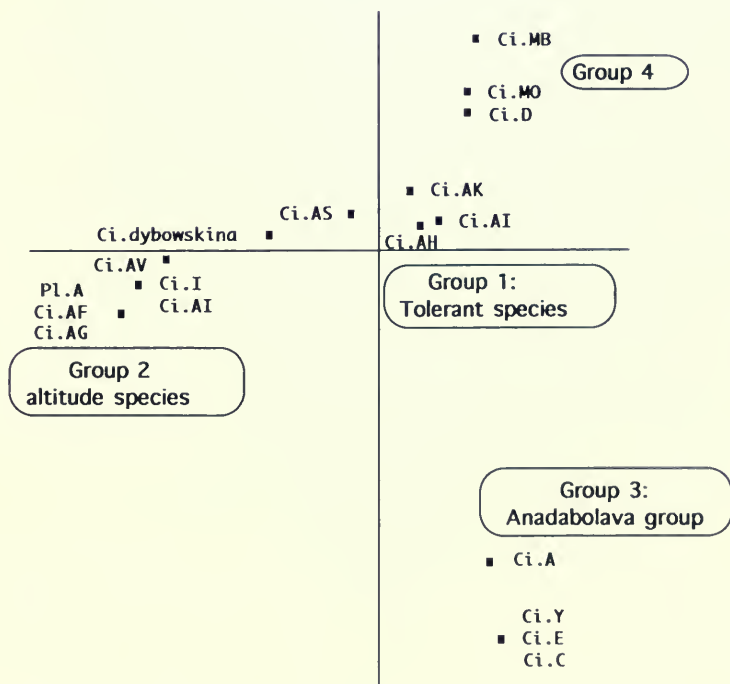


FIG. 5-2. Philopotamidae species of the Mandrare and Tarantzy basins plotted according to the first and second axes of correspondence analysis. For a key to the generic codes, see the legend to Figure 5-1. For species abbreviations see Table 5-1.

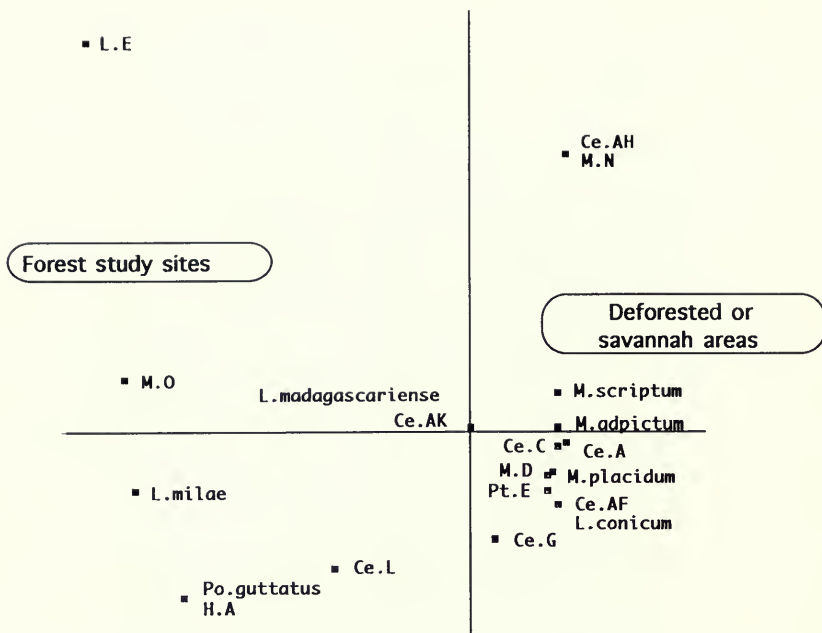


FIG. 5-3. Hydropsychidae species of the eastern basins plotted according to the third and fourth axes of correspondence analysis. For a key to the generic codes see the legend to Figure 5-1. For species abbreviations see Table 5-1.

which were only captured once at stations where no other species occurred) (Fig. 5-3); and (4) Philopotamidae species of eastern basins (from Efaho to Manampanihy) plotted according to the 2nd and 3rd axes (Fig. 5-4) (the 1st axis isolates *Chimarra* sp. C, which was captured only once on a small coastal tributary where no other species occurred).

The geographic distribution of some representative species of Philopotamidae (Fig. 5-5—*Chimarra* spp. and *Paulianodes* spp.) and Hydropsychidae (Fig. 5-6—*Cheumatopsyche* spp., *Macrostemum* spp., *Leptonema*, *Polymorphanisus*, *Hydropsyche*, and *Potamyia*) are presented.

Analysis and Discussion

Hydropsychidae, Western Region

Three groups of species related to three different ecological conditions can be distinguished from the analysis (Fig. 5-1).

The first group (*Macrostemum scriptum*, *M. adpictum*, *Cheumatopsyche* spp. AH and C) is composed of widespread species that are broadly distributed in Madagascar, especially in the western

and central regions of the island; they are able to endure significant variation in water level change between the dry and wet seasons and heavy loads of suspended material. One, two, or more constituting species of this group can be found over the complete scale of stream orders, and nearly across the whole basin (Fig. 5-6). Within the western region there are two localized exceptions that are presented as the second and third groups.

The second group (*Cheumatopsyche* sp. AF, *Leptonema conicum*, and *Leptonema* sp. G) is composed of species captured on the western slopes of Pic Trafonaomby (Fig. 5-6), where several variables, including lower temperatures, higher water velocities, heavier and more regular precipitation, and vegetation along the watercourse, create better ecological conditions for the benthic fauna.

The third group (*Cheumatopsyche* sp. L, *Macrostemum* spp. K and C) was characterized by only one station along a medium-sized stream (Fig. 5-6). This atypical element, called the Anadabolava group (from the name of the nearest locality), occupies a quite peculiar intermediate situation. Upstream, the rivers and their smaller tributaries undergo brutal level variations due to irregularity of rains and associated heavy loads of

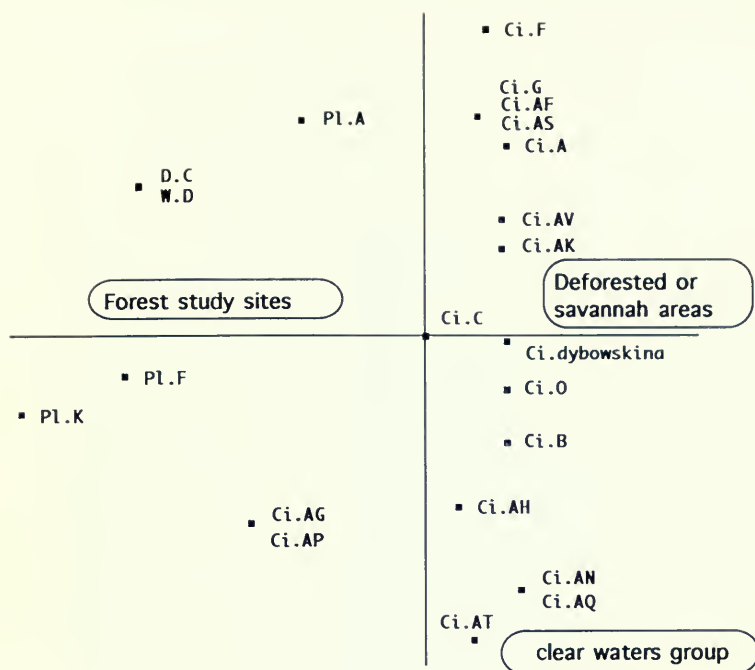


FIG. 5-4. Philopotamidae species of the eastern basins (from Efaho to Manampanihy) plotted according to the second and third axes of correspondence analysis. For a key to the generic codes see the legend to Figure 5-1. For species abbreviations see Table 5-1.

transported sediments. The fauna consists of a group 1 species (*Cheumatopsyche* sp. AH) that appears to be less particular in its habitat requirements. Downstream the river broadens, deepens, and rapids become rare; thus the conditions are less favorable for rheophile species. In the area of Anadabolava a large portion of the coarse suspended matter has already settled, and the river's output is more regular than on smaller tributaries although conditions are not yet really potamic. It is in this habitat that a narrow ecological niche probably exists. The zone described is poorly represented in this study but is suggested by the presence of three species found nowhere else on the Mandrare River.

Philopotamidae, Western Region

This analysis is a little more complicated than the previous one, but the general structure is similar (Fig. 5-2).
The first group is composed of two cosmopolitan and ubiquitous species (*Chimarra* spp. AH and AI). These two species are very tolerant of turbidity and water level variation, and they have

broad distributions, with the exception of the highest altitudes (Fig. 5-5).
The second group is constituted of species found on the higher slopes. These organisms were found on the western slope of Trafonaomby (as for Hydropsychidae) and on the high tributaries of the Mananara River. *Chimarra* sp. AS and *C. dybowskina* constitute a transition group between the two situations.
The third group (*Chimarra* spp. A, Y, C, and E) characterizes the Anadabolava study site (Fig. 5-5); there is a direct parallel to the Hydropsychidae and strong support for the preceding analysis. Three of the Philopotamidae species were found nowhere else during this study on the Mandrare River, and two of them (*Chimarra* spp. V and E) were scarce and probably characteristic of these clear, warm rivers.
The fourth group forms a distinct cluster and is composed of *Chimarra* spp. B, O, and D. On the basis of current information, this group does not have an equivalent among the Hydropsychidae. This atypical association, which is clearly distinguished from *Chimarra* sp. AS and *C. dybowskina*, can nevertheless occur in the same geographical and morphological conditions. Our hy-

Sampling sites and watercourses

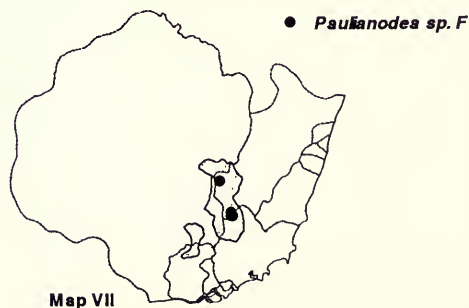
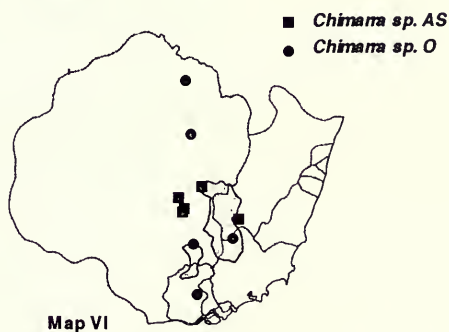
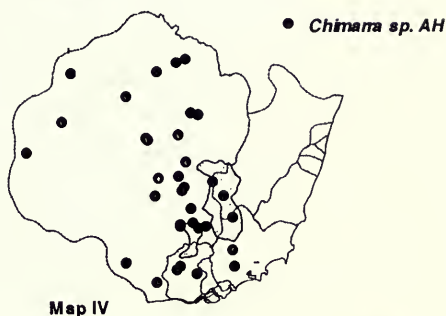
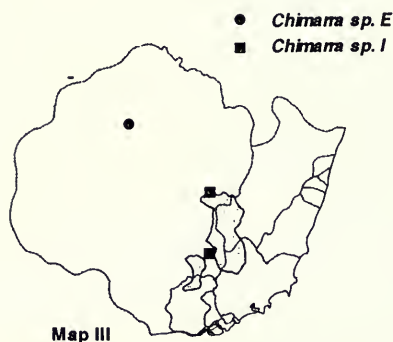
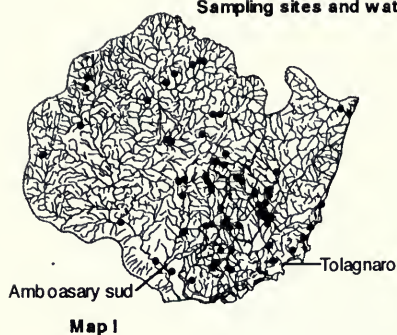


FIG. 5-5. Distributions of some representative species of Philopotamidae. Map I shows the watersheds of the region. Key to localities figured on Map II: 1—Mandrare Basin; 2—Manampanihy Basin; 3—Ebakika Basin; 4—Efaho Basin; 5—Tarantsy Basin; 6—small coastal basins; 7—RNI d'Andohahela (parcel 2); and 8—RNI d'Andohahela (parcel 1). Maps III–VI show the distributions of some representative species of Philopotamidae.

pothesis is that these species occupy sites whose vegetation (not the riparian vegetation, but that of the drainage area) is preserved. This hypothesis is supported by the few available data from other

basins. For example, before this work *Chimarra* sp. B was recorded only from small watercourses in the Zombitse Forest near Sakaraha (Elouard et al., 1994).

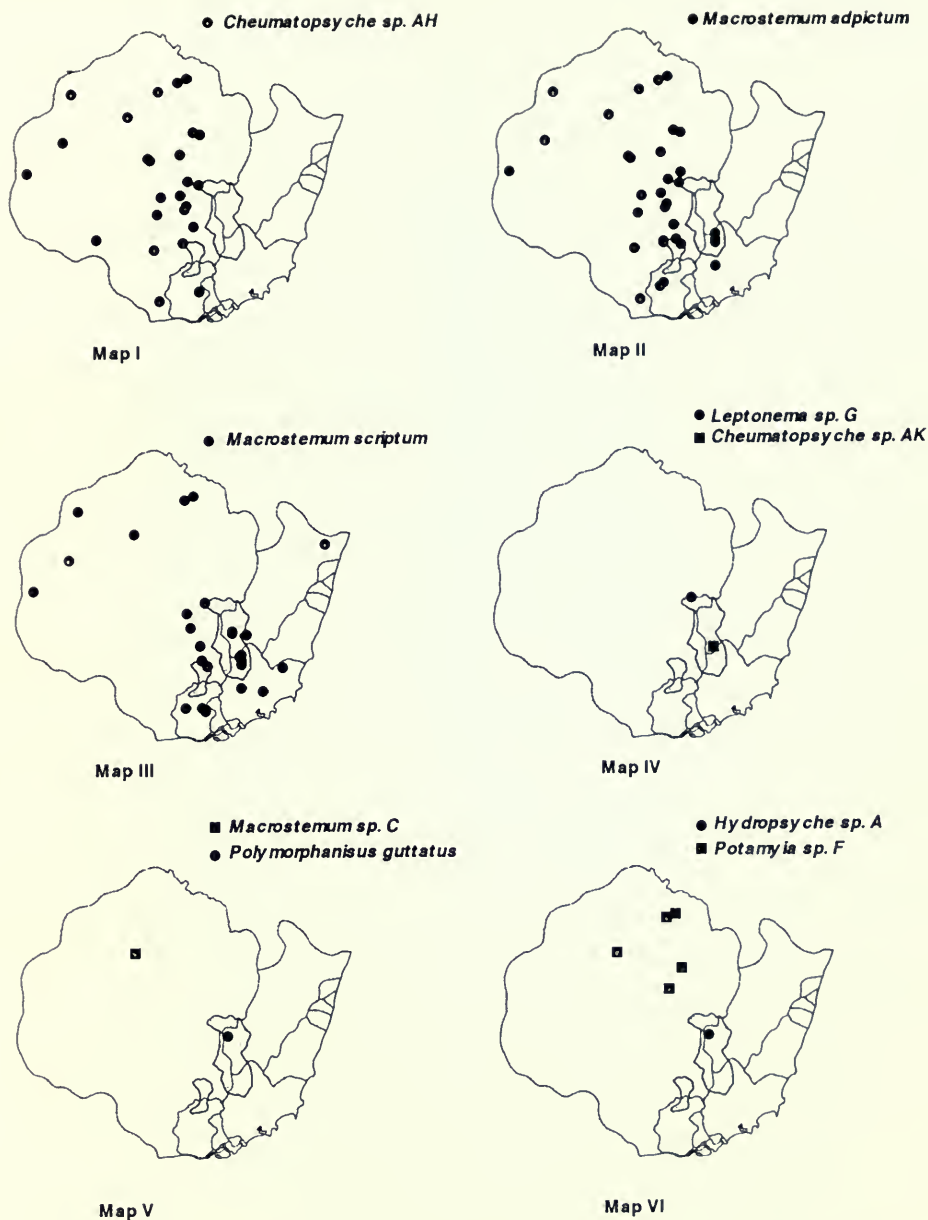


FIG. 5-6. Distributions of some representative species of Hydropsychidae (Maps I-VI).

Hydropsychidae, Eastern Region

The first axis of Figure 5-3 distinguishes two groups:

The first group corresponds to species living in the primary forest zones and the upper tributaries of the Manampanihy River. These species are roughly stratified according to elevation; the sec-

ond axis reflects an altitudinal gradient starting at about 500 m, where the genera *Polymorphanisus* and *Hydropsyche* were captured, and ending at 900 m, where *Leptonema* sp. E was obtained. The data are not extensive, and species richness along these slopes is probably underestimated. Nonetheless there is an altitudinal effect similar to that found on the Andringitra Massif (Gibon et al.,

1996). The significance of this result is fundamental for conservation—the eastern primary forests have an aquatic fauna that is unique and intolerant to changes in vegetational structure.

The second group corresponds to species associated with secondary forest, savannah, or agricultural areas. This fauna includes western species belonging to the first group, some of which penetrate slightly into the eastern area (e.g., *Cheumatopsyche* sp. AH), whereas others are common and broadly distributed (*Macrostemum* spp.). The species separation is based on the same gradient observed in the western region (from *Cheumatopsyche* sp. AH to *Leptonema conicum* and *Cheumatopsyche* sp. AF). The interpretation of this gradient, which is clearly linked with the altitude in the west region, is more ambiguous in the east; most of these sites are located between 50 and 120 m. Apparently, species restricted to high altitudes in the Mandrare Basin can also be found at much lower elevations in the east, where precipitation is more abundant and regular throughout the year. Once again, vegetation seems to play a major role. *Cheumatopsyche* sp. AH occurs in the agricultural coastal plain and *Leptonema conicum* and *Cheumatopsyche* and sp. AF occur in grassland and secondary forests.

Philopotamidae, Eastern Region

The results from this group confirm those from the Hydropsychidae, although new aspects of groupings appear that are more difficult to explain.

The first group is fauna of the primary forest. It is in the strict sense a world apart. Within this group each station has a unique fauna. As for the Hydropsychidae, this indicates that the data are probably incomplete and that speciosity is underestimated.

The second group is the fauna of secondary forest, savannah, or agricultural areas. Several of the sites have elements of the western fauna, but data are incomplete because some of the species were collected only once or twice. Furthermore, the environments are very diverse: they include a mosaic of secondary forests, cultivations, meadows, rice fields, etc. Thus, to properly analyze these different habitats, more samples are needed.

Even given these limitations in the data, several points are worth mentioning. Three eastern species (*Chimarra* spp. AN, AQ, and T) in this sample do not occur in the western region. Their oc-

currence is correlated with the presence of forest or with high elevations, but they are apparently associated with relatively clear waters. Our hypothesis is that they are found in savannah with low water turbidity either because they have descended from the upstream forest zone or because the vegetation, although for the greater part grass, is sufficiently dense to bind the soil and avoid erosion. These species are clearly distinguished from *Chimarra* sp. AS or *Chimarra dybowskiana*, both of which are generally associated with waters of high turbidity (e.g., in agricultural areas).

Conclusion

The longitudinal species distribution within hydrographical systems constitutes a fundamental ecological problem, but there are few studies of such situations from tropical zones (see Botosaneanu, 1979, and Malicky & Chantaramunkol, 1993). This near void in information is due to limited systematic studies of invertebrates and a lack of synthetic analyses for the little data that is available. In temperate regions, according to the theory of longitudinal zonation (Illies & Botosaneanu, 1963) or the river continuum concept (Minshall et al., 1985), faunistic transitions exist from the headwaters of rivers to their estuaries.

On the basis of the analysis presented here, the same pattern holds for the hydrological systems of southeastern Madagascar. However, at least two other factors affect the distribution of species or groups of species. The first, which we call the "Anadabolava effect," is a good example of the effect of intermediate human perturbation of the environment. The existence on the Mandrare River of a rich fauna wedged between irregular muddy upstream tributaries and a large homogeneous downstream river is one interesting result of this study. The second is the importance of intact vegetation and intact soil cover in the drainage area. The primary forests of RNI d'Andohahela have a rheophile fauna of Hydropsychidae and Philopotamidae. Local endemism for forest species of these families is very high (Gibon et al., 1996). Deforestation is followed by extreme faunistic changes, with the appearance of species resistant to high levels of suspended matter in the water. Beyond the question of the forest that was the aim of this paper and for which results are well defined, we suspect the existence of a species community inhabiting open ecosystems at low eleva-

tions, but requiring clear waters associated with weakly perturbed areas. This is an interesting topic for future hydrobiological research in the region.

Acknowledgments

The lack of a firm taxonomical basis for the organisms discussed herein is a major obstacle in quickly advancing this line of research. The sampling process is also tedious and often difficult. We are very grateful to those who have contributed and helped in many ways, in particular Fabienne Ranaivoharindriaka, Jean-Marc Elouard, Désiré Randriamasimanana, and Théogène Pilaka. We thank Fred Bastian and Steve Goodman for correcting the manuscript. This is contribution 10 of the "Biotypologie et biodiversité des eaux continentales malgaches" project, run jointly by CNRE and ORSTOM.

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Chapter 6

Proboscidoplocia (Ephemeroptera, Polymitarcyidae) from the Réserve Naturelle Intégrale d'Andohahela and Surrounding Areas, With a Description of a New Species

Jean-Marc Elouard,¹ Michel Sartori,² Jean-Luc Gattolliat,² and Ranalison Oliarinony¹

Abstract

A new species of *Proboscidoplocia* is described from the Réserve Naturelle Intégrale d'Andohahela, Madagascar. Two other species in the same genus, *P. vayssierei* and *P. ruffieuxae*, were also recorded within the reserve and nearby localities.

Résumé

Une nouvelle espèce de *Proboscidoplocia* est découverte dans la Réserve Naturelle Intégrale d'Andohahela. Les auteurs signalent la présence de *P. vayssierei* et *P. ruffieuxae* récoltés à l'intérieure et à l'extérieure de la réserve.

Introduction

Members of the genus *Proboscidoplocia* are the largest mayflies in the world and are endemic to Madagascar. Six species were recognized by Elouard and Sartori (1997). During the biological inventory of the Réserve Naturelle Intégrale (RNI) d'Andohahela in 1995 a previously undescribed species was collected. This mayfly is described below.

Proboscidoplocia mccaffertyi Elouard & Sartori, new species (Figs. 6-1 to 6-3)

Description of the Male Imago

BODY—Length without cerci = 24.9 mm.
HEAD—Transverse, completely black. L. =

0.38 mm; l. = 1.63 mm. Black eyes, located on the lateral extremity of the head capsule.

THORAX—Prothorax pale brown on the lateral tergite, whitish on the center. Its shape is tronconic, the narrower side behind the head. Meso- and metathoracic tergites greenish brown. Prothorax L. = 1.02 mm; l. ant. margin = 1.06 mm, l. post. margin = 1.7 mm; L. meso + metathorax = 13.5 mm.

FOREWINGS—Large and hyaline (Fig. 6-1a). Bordering cells of the posterior margin not very abundant and quite wide. Measurements in mm: L. = 15.9; l. = 8.4; L./l. = 1.89. Hindwings much smaller than the forewings, with few bordering cells (Fig. 6-1b). L. = 7.7; l. = 4.4; L./l. = 1.79. L. forewing/L. hindwing = 2.06.

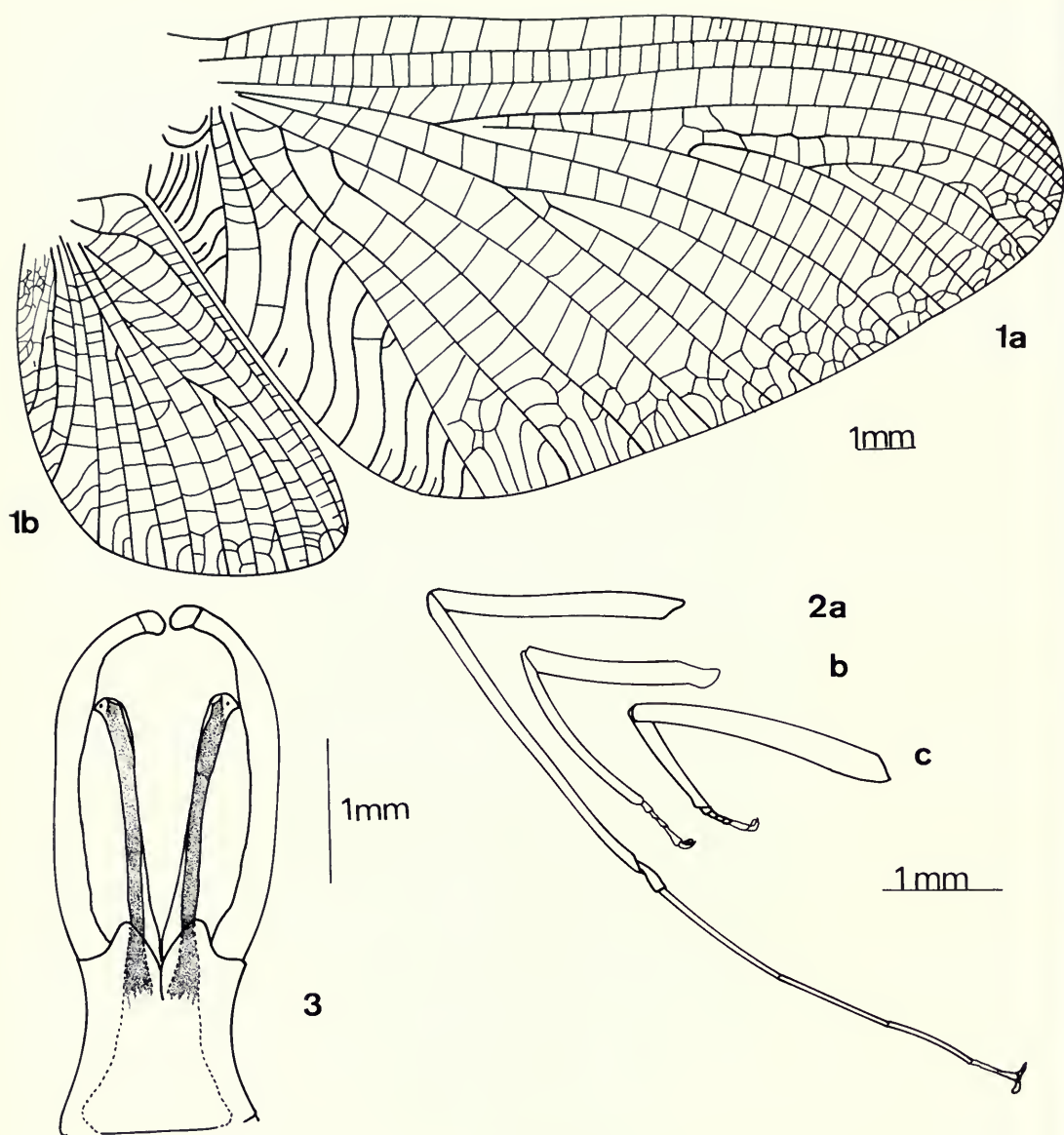
LEGS—Dark brown in color. Measurements presented in Table 6-1 and illustrations in Figure 6-2a to 6-2c.

ABDOMEN—Light brown. L. = 10 mm. Wide at the last abdominal segment l. = 1.16 mm.

GENITALIA (Fig. 6-3)—Two segmented forceps-like structures, basal segment long, L. = 2.48

¹ ORSTOM, B.P. 434, Antananarivo (101), Madagascar.

² Musée Cantonal de Zoologie, CP 448, CH-1000, Lausanne 17, Switzerland.



FIGS. 6-1 to 6-3. Illustrations of the holotype of *Proboscidoplocia mccaaffertyi*. (1a) Right forewing, (1b) right hindwing. (2a) Leg 1, (2b) leg 2, and (2c) leg 3. (3) Genitalia of the male imago, ventral view.

TABLE 6-1. Leg measurements (in mm) of *Proboscidoplocia mccaaffertyi* (see Fig. 6-2).

	Femora	Tibia	Total tarsus	Tarsus 1	Tarsus 2	Tarsus 3	Tarsus 4	Tarsus 5
P1	2.1	2.9		0.32	1.2	0.96	0.9	0.4
P2	1.6	1.6	0.5					
P3	2.1	0.96	0.38					



Sampled stations (84)



South-eastern basins



Proboscidoplocia mccaffertyi



Proboscidoplocia ruffieuxae



Proboscidoplocia vayssierei



Proboscidoplocia genus

FIGS. 6-4 to 6-9. Distribution of *Proboscidoplocia* species in the southeastern Malagasy basins. (4) Map of sampled stations and hydrographical network around the RNI d'Andohahela. (5) Localization of the southeastern basins and the position of the RNI d'Andohahela. (6) *Proboscidoplocia mccaffertyi*, sp. n.; (7) *P. ruffieuxae*; (8) *P. vayssierei*; (9) *Proboscidoplocia* spp. in general (nymphs, male and female imago).

mm; apical segment short, L. = 0.19 mm. Penis quite wholly black, very long, reaching three-quarters of the forceps length (L. = 1.6 mm) and joined only in the most basal part.

CERCI—Broken and missing.

This species differs from other members of the genus *Proposidoplocia* essentially by the length of the penis and its nearly total separation outside of the body. The most closely related species is *P. billi* Elouard and Sartori, 1997.

ETYMOLOGY—This species is dedicated to W. P.

McCafferty, one the world's specialists on Ephemeroidea.

HOLOTYPE—Sample P0538, 23 November 1995, station St41-09 (camp 1, Fig. 6-6; see Chapter 1), Manampanihy Basin, Andranohela River, 46°45'34"E, 24°36'43"S, 525 m. Body in alcohol and wings, legs, part of cerci, and genitalia on slide preparations. Deposited in the Laboratoire d'Entomologie du Muséum National d'Histoire Naturelle (MNHN), Paris.

PARATYPES—This species is known only from

the holotype. Some females and nymphs of this genus were recorded at the same station where the holotype of *Proboscidoplocia mccaffertyi* was collected, but for the time being we cannot assume that they belong to the same species.

Other *Proboscidoplocia* Species Recorded

Two other previously described *Proboscidoplocia* species were recorded in the RNI d'Andohahela. *Proboscidoplocia vaissyerei* Elouard and Sartori, 1997, was found in three streams near camp 1 in the forest zone of the upper part of the Manampanihy Basin. The elevation was around 525 m (Fig. 6-8). *Proboscidoplocia ruffieuxae* Elouard and Sartori, 1997, was obtained at several collecting stations of the Manampanihy Basin, one at 100 m outside of the reserve and the other at 525 m within a forested region of the reserve; at two sites in the Efaho Basin, at 70 and 120 m; and at one station in the upper streams of the Mandrare Basin, at 725 m (Fig. 6-7). Unidentified nymphs were recorded at numerous stations within and outside of the RNI d'Andohahela (Fig. 6-9). At this point we are unable to determine to which species these nymphs belong.

Discussion

Proboscidoplocia spp. live mainly in fresh-running rivers along the eastern coast and in the rivers of the upper basins of western Madagascar. Generally, they prefer clear forest streams with a current speed varying between 0.5 and 1.5 m/sec. Some species occur in small streams, while others frequent large rivers. In general, *Proboscidoplocia* species along the west coast occur at higher elevations than their congeners in eastern Madagascar. An abundance of rain, suitable air and wa-

ter temperatures, and the presence of forest are probably important factors that affect the distribution and greater speciosity of this genus in the eastern portion of the island.

The presence in the southeast of *Proboscidoplocia* on the Manampanihy River and close to (but outside of) a forested area is probably due to the influence of the nearby forest, which provides cooler water and a flow of rich organic material in the streams. Apart from collection sites located within forest areas of the reserve or in its immediate vicinity, *Proboscidoplocia* is absent from the lower part of the Mandrare, Manampanihy, and Efaho basins (Fig. 6-5). Thus, these organisms are completely dependent on the intact forests of southeastern Madagascar for their continued existence.

Acknowledgments

This study represents contribution 11 of the project "Biotypologie et biodiversité des eaux continentales malgaches," run jointly by CNRE and ORSTOM. The program is financed through the French Fonds d'Aide et de Coopération (FAC). We thank our colleagues at Laboratoire de Recherche sur les Systèmes Aquatiques et leur Environnement (LRSAE) for their help and assistance. We are deeply indebted to the Ministère de la Recherche Appliquée au Développement (MRAD) for the facilities made available to our research program. Maps were drawn with the CartoNOE software, written by O. Hertu.

Literature Cited

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Chapter 7

Three New Species of Baetidae (Ephemeroptera) from the Réserve Naturelle Intégrale d'Andohahela, Madagascar

Jean-Luc Gattolliat,¹ Michel Sartori,¹ and Jean-Marc Elouard²

Abstract

Two new species of *Afroptilum* (Ephemeroptera: Baetidae) are described from the imaginal stage and for one species of *Dabulamanzia* (Ephemeroptera: Baetidae) from the nymphal and imaginal stages from the Réserve Naturelle Intégrale d'Andohahela. Affinities and ecology are discussed.

Résumé

Deux nouvelles espèces d'*Afroptilum* (Ephemeroptera: Baetidae) de la Réserve Naturelle Intégrale d'Andohahela sont décrites à partir des imagos et une espèce de *Dabulamanzia* (Ephemeroptera: Baetidae) à partir de la larve et de l'imago. Leurs affinités et leur écologie sont discutées.

Introduction

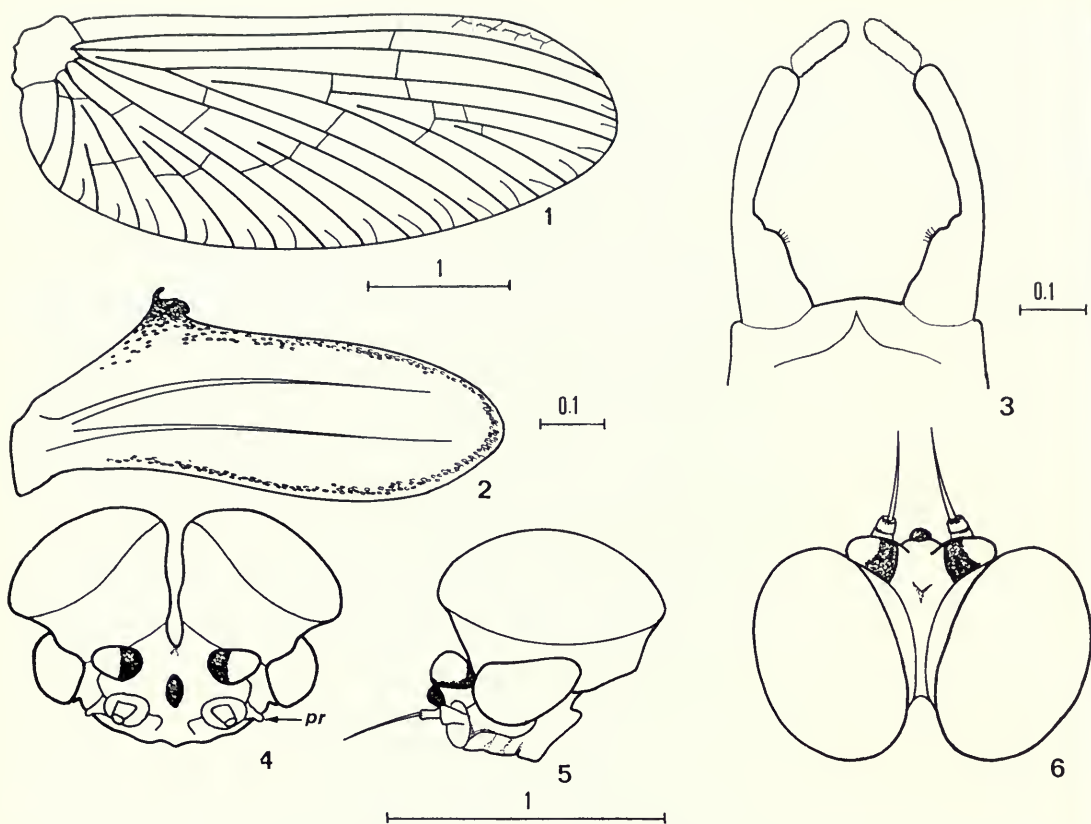
Very few taxonomic works have been carried out on Malagasy Baetidae. Eleven species belonging to five genera have been described to date. Over the course of the past 6 years, a program organized by the Office de la Recherche Scientifique et Technique Outre-mer (ORSTOM) and Centre National de la Recherche Scientifique (CNRS) entitled "Biotypologie et biodiversité des eaux continentales malgaches" has sought to add information on the organisms inhabiting freshwater ecosystems in Madagascar. We currently estimate that 40 baetid species occur on the island.

Three new species from the Réserve Naturelle Intégrale (RNI) d'Andohahela are discussed in this paper. Two of these species are placed in the

genus *Afroptilum* Gillies, 1990, based on the forewing venational pattern, especially the presence of single intercalary veins and two spurs on the hindwings (Gillies, 1990). These two species differ from species of *Centroptilum* Eaton, 1869, in the shape of the second and third segments of the forceps, the second segment becoming narrower at the apex and the third elongated instead of globular, as in *Centroptilum* (Gillies, 1990), and in the lack of a prominent median spine between the gonopod bases (McCafferty & Waltz, 1990). Generic attribution is provisional because knowledge of the nymphal stage is limited; such information might be helpful in understanding the relationships of these two species. The third species is placed in the genus *Dabulamanzia* Lugo-Ortiz and McCafferty, 1996. This generic allocation is justified because the larval stage has a bulbous labial segment 3 and proximal arc setae on the tibia. Furthermore, at the imaginal stage the hindwings have a hooked spur and three longitu-

¹ Musée Cantonal de Zoologie, CP 448, CH-1000, Lausanne 17, Switzerland.

² ORSTOM, BP 434, Antananarivo (101), Madagascar.



FIGS. 7-1 through 7-6. *Afroptilum mathildae*, new species; male imago. (1) forewing, (2) hindwing, (3) genitalia, (4) head in frontal view (pr = process), (5) head in lateral view, (6) head in dorsal view. Scales are in millimeters.

dinal veins, and the male genitalia gonopods have a basomedial projection on segment 2 (Lugo-Ortiz & McCafferty, 1996). A major systematic revision of African Baetidae is about to be completed (McCafferty, pers. comm.).

The holotypes and part of the paratype series are housed in the Musée Cantonal de Zoologie, Lausanne, Switzerland. Other paratypes are deposited in the Museum National d'Histoire Naturelle (MNHN), Paris, and CNRE, Antananarivo.

Descriptions

Afroptilum mathildae Gattolliat & Sartori, new species (Figs. 7-1 to 7-6)

Male Imago

BODY LENGTH (WITHOUT CAUDAL FILAMENTS)—4.7 mm (4.3–5.2).

HEAD—Width, 1.0 mm. Uniform light brown with a dark brown trapezoid figure between compound eyes (Fig. 7-6). Turbinate eyes uniformly dark brown–purple, well separated and becoming narrower posteriorly (Fig. 7-5). Well-marked process lateral to each antenna (Fig. 7-4). Antennae uniformly pale cream.

THORAX—Light brown with only margins of sclerites darker brown.

FOREWINGS—Mean length, 4.8 mm (4.4–5.4); mean width, 1.9 mm (1.7–2.2); length/width ratio, 2.5. Membrane opaque except distal third of costal area light gray. Pterostigma with four to six horizontal and vertical cross-veins. One intercalary vein between longitudinal veins except between subcostal and first radial veins (Fig. 7-1).

HINDWINGS—Mean length, 0.8 mm (0.7–0.9); mean width, 0.2 mm (0.2–0.3); length/width ratio, 3.2. Fore- to hindwing ratio, 6.2. Membrane hyaline with micropores near margin resembling a black border. Two prominent longitudinal veins

TABLE 7-1. Measurements (mm) of *Afroptilum mathildae*, new species.

	Femur	Tibia	Tarsus and claw
P1	0.80	1.58	1.21
P2	0.73	0.95	0.42
P3	0.73	0.89	0.42

joined at base. Costal projection with two spurs, upper clearly thinner than lower (Fig. 7-2).

LEGS—Light brown without markings. Measurements are presented in Table 7-1.

ABDOMEN—Pale cream, each segment with a double black lateral line that widens at two-thirds length.

GENITALIA—Three-segmented gonopods, segmentation between first and second segment not well differentiated. Length of segments 1 and 2, 0.4 mm; that of segment 3, 0.1 mm. First segment larger than others with a brush of setae on internal apical margin. Third segment elongated, slightly grooved (Fig. 7-3).

Examined Material

HOLOTYPE—One male imago (no. 405-11), 23 April 1995, Antorendrika Basin, Antorendrika River, locality Belavenoka, St89-17 (LRSAE/ORSTOM station code; see Chapter 5), Madagascar, 47°05'02"E, 24°50'18"S, 20 m.

PARATYPES—Three male imagos (nos. 405-9, 405-12, and 405-18), 23 April 1995, Antorendrika Basin, Antorendrika River, locality Belavenoka, St89-17, Madagascar, 47°05'02"E, 24°50'18"S, 20 m. Fifty male imagos in alcohol, 23 April 1995, Antorendrika Basin, Antorendrika River, locality Belavenoka, St89-17, Madagascar, 47°05'02"E, 24°50'18"S, 20 m.

OTHER EXAMINED MATERIAL—Two male imagos (nos. 87-4 and 87-5), 13 April 1992, Mandrare Basin, Mandrare River, St12-03, Madagascar, 46°18'30"E, 24°13'18"S. One male imago (no. 91-9), 15 April 1992, Manampanihy Basin, tributary of Manampanihy River, locality Fenoevo, St41-01, Madagascar, 46°53'39"E, 24°41'00"E, altitude 72 m. One male imago (no. 526-6), 21 November 1995, Manampanihy Basin, Manampanihy River, locality Enosiary, St41-06, Madagascar, 46°49'19"E, 24°40'37"S. One male imago (no. 548-8), 29 November 1995, Manampanihy Basin,

Manampanihy River, locality Enosiary, St41-06, Madagascar, 46°49'19"E, 24°40'37"S, 100 m.

Ecology

This species has been found in rivers and streams flowing in woody savannah, steppe, and degraded forest areas. It has been captured with evening light traps, and with morning light traps in stations at low altitude. At one station it was the most abundant mayfly, with more than 200 male imagos caught in one evening.

Afroptilum gilberti Gattolliat & Sartori, new species (Figs. 7-7 to 7-12)

Male Imago

BODY LENGTH (WITHOUT CAUDAL FILAMENTS)—5.0 mm (4.7–5.2).

HEAD—Width, 1.2 mm. Light brown with a dark brown patch between compound eyes (Fig. 7-12) and brown marks on lower margin of carena between antennae (Fig. 7-10). Turbinate eyes light brown except dark brown base. Pale cream antennae with dark brown marks on segments 1, 2, and 3. Well-developed carena prolonged clearly below antennae (Fig. 7-11).

THORAX—Light brown, with only margin of sclerites darker brown.

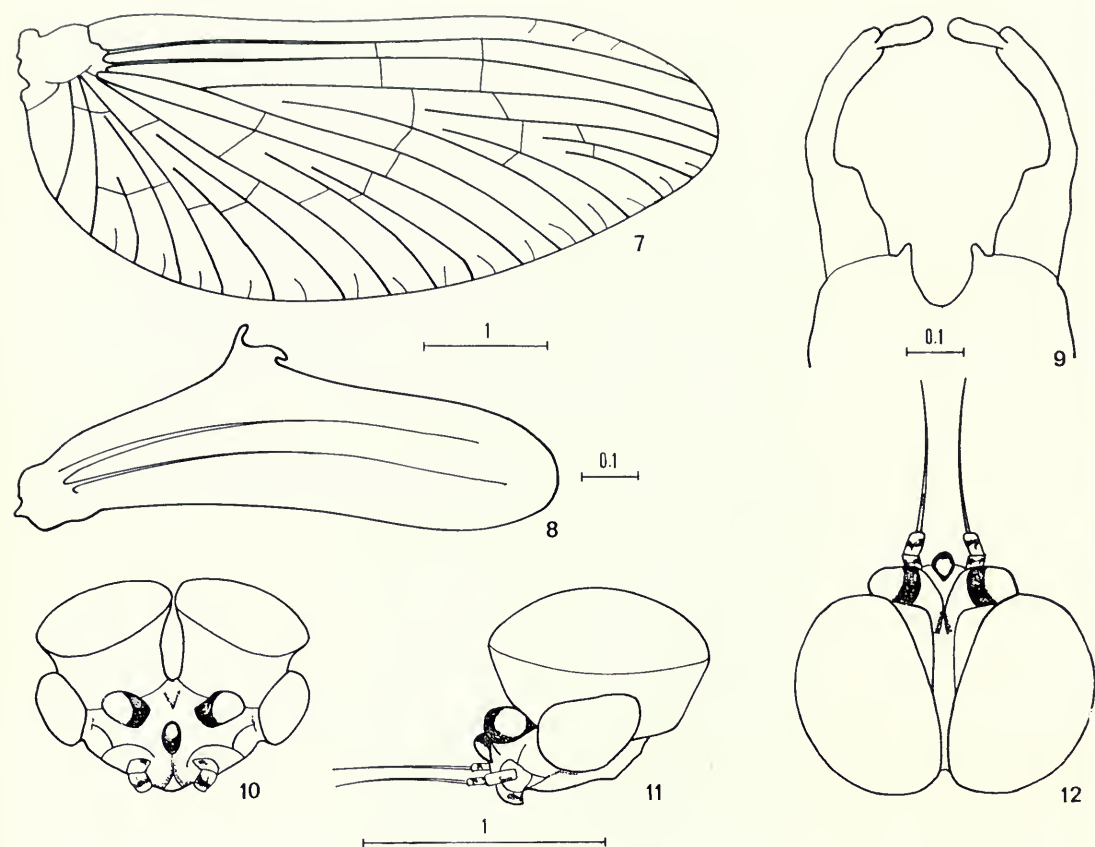
FOREWINGS—Mean length, 5.3 mm (5.1–5.9); mean width, 2.1 mm (2.0–2.1); length/width ratio, 2.5. Membrane opaque except apical third of costal region light gray. Pterostigma with three to seven vertical cross-veins. One intercalary vein between longitudinal veins except sometimes between subcostal, first, second, and third radial veins (Fig. 7-7).

HINDWINGS—Mean length, 0.9 mm (0.8–0.9); mean width, 0.3 mm (0.2–0.3); length/width ratio, 3.2. Fore- to hindwing ratio, 6.0. Membrane hyaline without micropores. Two longitudinal veins well marked and joined at the base. Two spurs clearly distinguishable (Fig. 7-8).

LEGS—Pale cream with brown marks on femora and tibiae. Measurements are presented in Table 7-2.

ABDOMEN—Pale cream, with a brown narrow line at distal margin of each segment and a black lateral patch in the middle of each segment.

GENITALIA—Three-segmented gonopods, segmentation between first and second segment bare-



FIGS. 7-7 through 7-12. *Afropertilum gilberti*, new species; male imago. (7) forewing, (8) hindwing, (9) genitalia, (10) head in frontal view, (11) head in lateral view, (12) head in dorsal view. Scales are in millimeters.

ly visible. Length of segment 1 and 2, 0.4 mm; segment 3, 0.1 mm. First segment very large becoming narrow only at apex, with an apophysis at base (Fig. 7-9). Third segment elongated, un-streaked.

Examined Material

HOLOTYPE—One male imago (no. 546-3), 27 November 1995, Manampanihy Basin, Andrano-

hela River, locality camp 2 (see Chapter 1), St41-12, Madagascar, 46°44'25"E, 24°35'47"S, 810 m.

PARATYPES—One male imago (no. 91-6), 15 April 1992, Manampanihy Basin, tributary of Manampanihy River, locality Fenoovo, St41-01, Madagascar, 46°53'39"E, 24°41'00"S, 72 m.

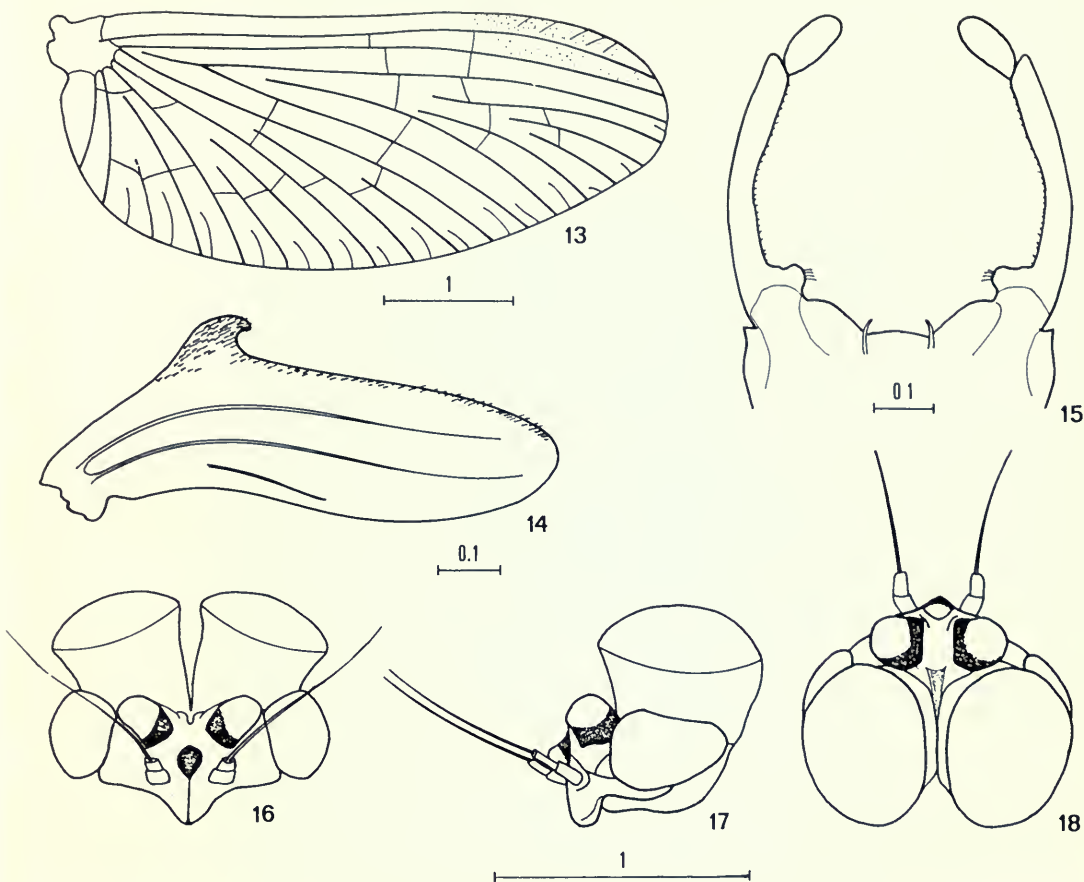
OTHER MATERIAL—One male imago (no. 341-13), 3 June 1994, Mandrare Basin, Marotoko River, locality 2 km from Mananara, St12-20, Madagascar, 46°38'50"E, 24°44'02"S, 275 m. One male imago (no. 525-7), 20 November 1995, Efa-ho Basin, Ambahibe River, locality Isaka-Ivondro, St89-05, Madagascar, 46°51'53"E, 24°46'47"S, 70 m.

TABLE 7-2. Measurements (mm) of *Afropertilum gilberti*, new species.

	Femur	Tibia	Tarsus and claw
P1	1.02	2.05	1.84
P2	0.82	1.21	0.53
P3	0.79	1.16	0.49

Ecology

This species has been found in a variety of ecological settings from flowing streams in intact humid forest to degraded forest, and at mid- to low



FIGS. 7-13 through 7-18. *Dabulamanzia duci* new species; male imago. (13) forewing, (14) hindwing, (15) genitalia, (16) head in frontal view, (17) head in lateral view, (18) head in dorsal view. Scales are in millimeters.

elevations. It was seldomly captured, and only in the evening with light traps. The species is apparently rare and has been found only in or close to the RNI d'Andohahela (Fig. 7-31). It is almost certainly very sensitive to forest destruction and the ensuing ecological changes within the stream ecosystem.

Dabulamanzia duci Gattolliat & Elouard, new species (Figs. 7-13 to 7-28)

Male Imago

BODY LENGTH (WITHOUT CAUDAL FILAMENTS)—5.0 mm (4.8–5.6).

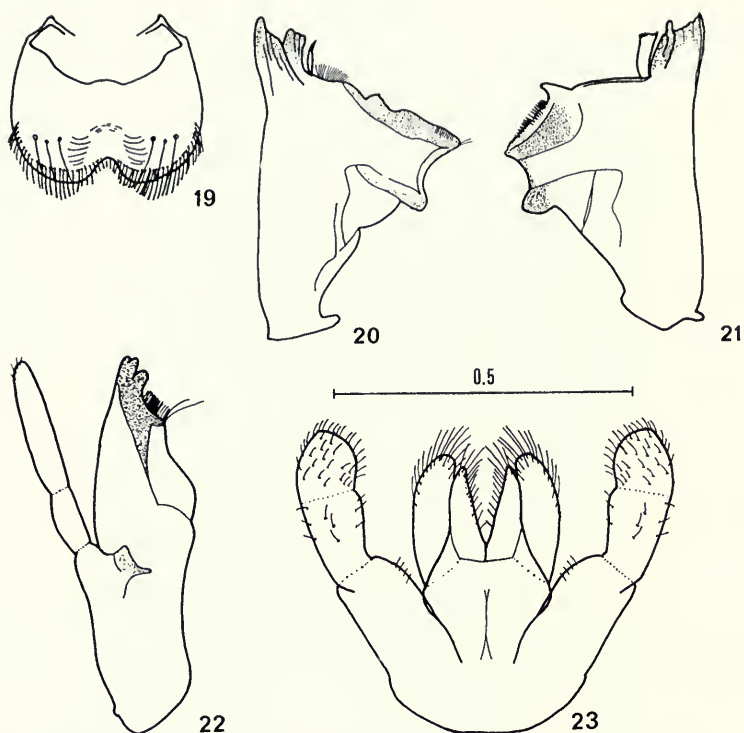
HEAD—Width, 1.1 mm. Light brown with a dark brown patch between lateral ocelli and turbinate eyes (Fig. 7-18). Turbinate eyes deep orange (becoming honey-brown after preservation

and storage in alcohol), subcylindrical. Stout carena between antennae (height of carena equals distance between antennae; Fig. 7-17). Flagella of antennae quite long, but not always as long as shown in Figure 7-16. The peculiar shape of the head and the color of the eyes are typical of this species.

THORAX—Uniformly pale cream.

FOREWINGS—Mean length, 4.6 mm (4.0–5.0); mean width, 1.9 mm (1.6–2.1); length/width ratio, 2.4. Membrane opaque except apical third of costal region light gray. Pterostigma with five to seven vertical cross-veins. One intercalary vein between longitudinal veins except between subcostal and first radial veins and generally also between the second and third radial veins (Fig. 7-13).

HINDWINGS—Mean length, 0.8 mm (0.7–0.9); mean width, 0.2 mm (0.2–0.3); length/width ratio, 3.7. Fore- to hindwing ratio, 5.7. Membrane hy-



FIGS. 7-19 through 7-23. *Dabulamanzia duci*, new species; male nymph. (19) labrum, (20) right mandible, (21) left mandible, (22) right maxilla, (23) labium. Scale is in millimeters.

aline. Two longitudinal veins well-marked and generally joined at base, distinctly more prominent than the nonintersecting third vein. Costal projection with only one developed spur. Small teeth covering the whole outer margin of wings (Fig. 7-14).

LEGS—Pale cream without mark. Measurements are presented in Table 7-3.

ABDOMEN—Pale cream, with a brown, narrow, transverse line on posterior margin of each segment.

GENITALIA—Three-segmented gonopods, segmentation between first and second segments barely visible. Length of segments 1 and 2, 0.4 mm; segment 3, 0.05 mm. Second segment long, with a stout apophysis bearing a brush of setae, the inner margin covered with small teeth. Third segment ovoid and elongated (Fig. 7-15).

Female Imago

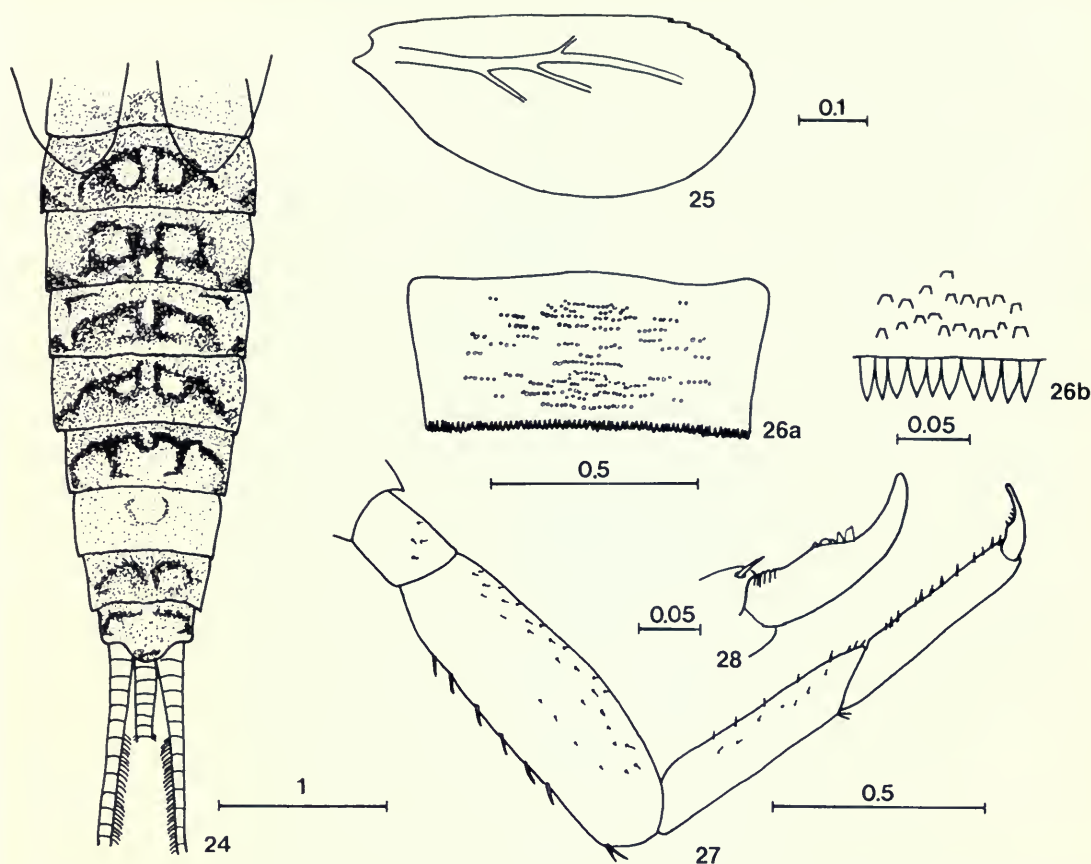
No significant differences in size or color compared to the male imago. The hindwings with their spur on the costal margin and the three longitu-

dinal veins are useful characters by which to recognize females of this species.

Nymph

BODY LENGTH (WITHOUT CAUDAL FILAMENTS)—5.6 mm.

MOUThPARTS—Dorsal surface of labrum with fine setae along apical margin, three larger setae on each side and reaching the margin (Fig. 7-19). Canines of right mandible not fused, with very small teeth, a large brush of setae between canines and molars (Fig. 7-20). Canines of left mandible not fused (Fig. 7-21). Maxillary palpi two-segmented and as long as galea-lacinia, second segment elongated with a few fine setae at apex. Apical teeth of maxillae broad, brush of setae with two or three longer ones at inner margin, no sensory hair behind apical teeth (Fig. 7-22). Labial palpi stout and composed of three segments partially fused; setae covering third segment, scarce on first and second segments, and inner margin of second segment slightly convex distally. Glossae as long as paraglossae (Fig. 7-23).



FIGS. 7-24 through 7-28. *Dabulamanzia duci*, new species; male nymph. (24) abdomen in dorsal view, (25) left gill III, (26a) segment VIII in dorsal view, (26b) posterior margin of segment VIII in dorsal view, (27a) left leg, (27b) claw on the left leg. Scale is in millimeters.

LEGS—Femora with six large bristles on outer margin and a couple of distal bristles, upper surface with scattered spine-like bristles; no femoral patch of setae. Tibiae with sparse scattered spine-like bristles on outer margin, a couple of bristles at apex, without a dorsal line of fine setae (Fig. 7-28c). Tarsi with a line of spine-like setae, claws with one row of about five teeth (Fig. 7-28d).

ABDOMEN—Light brown with dark brown marks on each segment (Fig. 7-24). Each segment

with scale bases and posterior margin with triangular spines longer than wide (Fig. 7-27a, b). Gills present on segments I–VII, asymmetrical and relatively elongated, serrated at apex, tracheation with few ramifications (Fig. 7-25). Presence of cerci and median filament (broken at one-quarter length of cerci), cerci with hair only on interior side, median filament hairs on both sides (Fig. 7-24).

TABLE 7-3. Measurements (mm) of *Dabulamanzia duci*, new species.

	Femur	Tibia	Tarsus and claw
P1	1.13	1.95	2.05
P2	0.84	1.05	0.62
P3	0.79	1.00	0.52

Examined Material

HOLOTYPE—One male imago (no. 525-5), 20 November 1995, Efaho Basin, Ambahibe River, locality Isaka-Ivondro, St89-05, Madagascar, 46°51'53"E, 24°46'47"S, 70 m.

PARATYPES—One male imago (no. 525-6), 20 April 1995, Efaho Basin, Ambahibe River, locality Isaka-Ivondro, St89-05, Madagascar, 46°51'53"E,

24°46'47"S, 70 m. One female imago and four males imagos (nos. 91-10, 91-2, 91-3, 91-4, and 91-5), 15 April 1992, Manampanihy Basin, tributary of Manampanihy River, locality Fenoevo, St41-01, Madagascar, 46°53'39"E, 24°41'00"S, 72 m. One nymphal exuvia with the corresponding male subimago (no. 339-31) and one male imago (no. 339-18), 2 June 1994, Mandrare Basin, Mananara River, locality Hazofotsy, St12-17, Madagascar, 46°35'46"E, 24°48'57"S, 100 m.

OTHER EXAMINED MATERIAL—One male imago (no. 90-8), 14 April 1992, Efaho Basin, Efaho River, locality Ifarantsa, St89-01, Madagascar, 46°52'12"E, 24°55'37"S, 20 m. One male imago (no. 341-12) and seven male individuals, 3 June 1994, Mandrare Basin, Marotoko River, locality 2 km after Mananara, St12-20, Madagascar, 46°38'50"E, 24°44'02"S, 275 m. Three male imagos (nos. 343-5, 343-6, and 343-7), 5 June 1994, Mandrare Basin, Manambolo River, locality 7 km from Berohangana, St12-22, Madagascar, 46°35'11"E, 24°35'07"S, 440 m. One male imago (no. 514-4), 19 October 1995, Rianila Basin, unnamed river, locality road to Lakato, St17-31, Madagascar, 48°21'48"E, 19°02'40"S, 1050 m. One male imago (no. 525-5), 20 November 1995, Efaho Basin, Ambahibe River, locality Isaka-Ivondro, St85-05, Madagascar, 46°51'53"E, 24°46'47"S, 70 m. One male imago (no. 569-1), 2 February 1996, Mandrare Basin, Sakamalio River, locality RNI d'Andohahela, St12-38, Madagascar, 46°40'56"E, 24°32'07"S, 750 m. Three male imagos (nos. 607-1, 607-2, and 607-3), 5 October 1996, Lokoho Basin, unnamed river, locality RNI d'Marojejy (Camp 1), St44-04, Madagascar, 49°46'18"E, 14°25'50"S, 500 m. Three male imagos (nos. 614-1, 614-2, and 614-3), 11 November 1996, Lokoho Basin, Manantenina River, locality RNI d'Marojejy (Camp 1), St44-03, Madagascar, 49°46'20"E, 14°26'02"S, 450 m. Two male imagos (nos. 619-2 and 619-3), one subimago male (no. 619-4), 13 October 1996, Lokoho Basin, Manantenina River, locality RNI d'Marojejy (Camp 1), St44-03, Madagascar, 49°46'20"E, 14°26'02"S, 450 m.

Ecology

Dabulmanzia duci is one of the most common and widespread species of Baetidae in southeastern and eastern Madagascar. It has been found from sea level to above 1000 m, in streams and rivers flowing in all types of vegetation, and in-

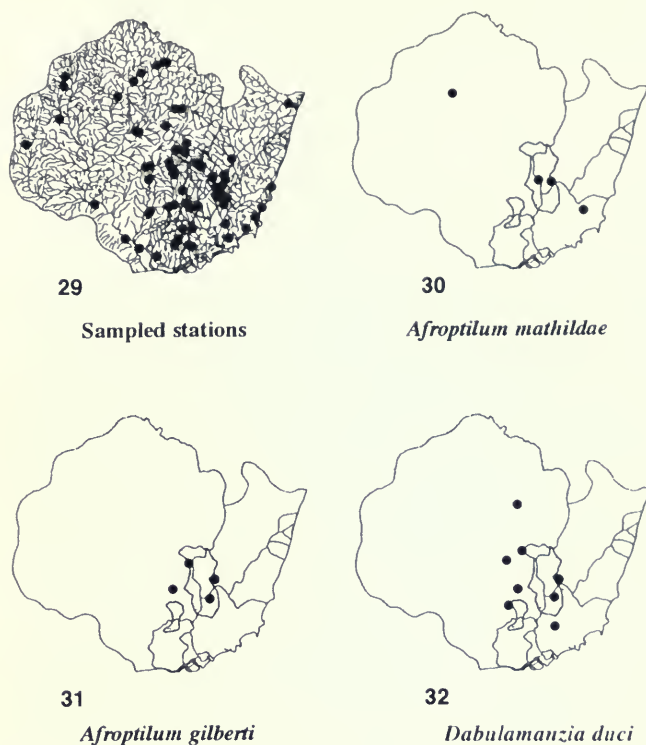
side and outside of the RNI d'Andohahela (Fig. 7-32). It was captured with evening and morning light traps, as well as with hand nets during the morning. The males fly in a quite peculiar manner: they apparently wait for the females in horizontal flight a few centimeters above flat stones or rocks.

Affinities

Only one related species has been described from Madagascar: *Afroptilum* (*Centroptilum*) *electropterus* (Demoulin, 1966). *Afroptilum mathildae* and *A. gilberti* differ from *A. electropterus* by the presence of two spurs on the hindwings (instead of one in *A. electropterus*), by the shape of the gonopods, and by the size and color of the turbinate eyes. *Dabulamanzia duci* differs from *A. electropterus* by the presence of three veins in the hindwings (only two in *A. electropterus*), the shape of the genitalia, and the color of the eyes (Demoulin, 1966).

Afroptilum mathildae and *A. gilberti* are much closer to *A. decipiens* subgenus *Afroptilum*, group *sudafricanum* Gillies, 1990, but the shape of the two spurs on the hindwings and especially the shape of the first and second segments of the gonopods are quite different. *Afroptilum gilberti* differs from *A. mathildae* by the color of the turbinate eyes, the presence of a carena between the antennae, and the absence of a brush of setae on the margin of the first segment of the gonopods.

Dabulamanzia duci is closer to *D. tarsale* (Gillies, 1990), previously assigned to the *tarsale* group of *Afroptilum*. However, *D. duci* differs from *D. tarsale* by eye color and by the shape of the third segment of the gonopods, which is shorter and more ovoid in *D. duci*. *Dabulamanzia duci* is also relatively similar in morphology to *D. babaora* (Wuillot & Gillies, 1993), except for differences in the shape and the size of the first segment of the gonopods. The nymph is also very similar to that of *D. babaora*, but the mandibles and the labial palpi are different. *Dabulamanzia duci* is easily distinguished from *D. fica* and *D. helenae* by the shape and number of teeth of the claws (Lugo-Ortiz & McCafferty, 1996). *Dabulamanzia duci* is easily distinguished from *A. mathildae* and *A. gilberti* by the shape of the head, the color of the eyes, the shape of the first segment of the gonopods, and especially by the number of longitudinal veins in the hindwings.



FIGS. 7-29 through 7-32. Distribution of some *Afroptilum* and *Dabulamanzia* in basins of southeastern Madagascar. The gray area delimits parcels 1 and 2 of the RNI d'Andohahela. (29) sampled stations, (30) distribution of *A. mathildae*, (31) distribution of *A. gilberti*, (32) distribution of *D. duci*.

Discussion

The three new species of Baetidae described herein have different spatial and ecological distributions. *Afroptilum mathildae* is typically a species of low altitude, locally abundant in large rivers (Fig. 7-30). Its presence in other basins along the eastern coast needs to be confirmed. At the opposite extreme is *A. gilberti*, a species that lives in small and well-oxygenated streams; its distribution is directly related to the presence of forest, and it has been found only in or around the RNI d'Andohahela (Fig. 7-31). Its future existence depends completely on these environmental conditions and consequently on the preservation of the forest. *Dabulamanzia duci* is a widespread species, found in large and small streams along the eastern and southeastern coasts. It is known from areas within and outside of the RNI d'Andohahela (Fig. 7-32). Owing to its capacity to thrive in a variety of environments, this species is not endangered by forest degradation. At least 15 new species of Baetidae have been collected in recent years in southeastern Madagascar. Descriptions of

these animals and information on their ecology will be the subject of future articles.

Acknowledgments

This study represents contribution no. 12 of the "Biotypologie et biodiversité des eaux continentales malgaches" project, run jointly by CNRE and ORSTOM. The program is financed through the French Fonds d'Aide et de Coopération (FAC). We thank our colleagues at Laboratoire de Recherche sur les Systèmes Aquatiques et leur Environnement (LRSAE) for their help and assistance. We are deeply indebted to the Ministère de la Recherche Appliquée au Développement (MRAD) for the facilities made available for our research program. The text of a previous version of this chapter was substantially improved by comments by Steve Goodman and an anonymous reviewer.

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Chapter 8

Aquatic Biodiversity of Madagascar: *Simulium* (Diptera: Simuliidae) from the Réserve Naturelle Intégrale d'Andohahela and Surrounding Areas

Théogène Pilaka¹ and Jean-Marc Elouard¹

Abstract

The distribution of species of the genus *Simulium* (Diptera: Simuliidae) in rivers situated inside and outside the Réserve Naturelle Intégrale d'Andohahela is reviewed. No new species were discovered during the inventory of the reserve.

Résumé

Les auteurs étudient la distribution du genre *Simulium* (Diptera: Simuliidae) dans les rivières situées à l'intérieure et à l'extérieure de la Réserve Naturelle Intégrale d'Andohahela. Aucune espèce nouvelle n'a été découverte à l'intérieure de la réserve.

Introduction

The hydrographic network of southeastern Madagascar, including many rivers that have their origins in the hills making up the Réserve Naturelle Intégrale (RNI) d'Andohahela, comprises five main drainage systems: the Mandrare, the Efaho, the Tarantsy, the Ebakika, and the Manampanihy basins. The eastern portion of this region has, on the higher slopes, relatively intact primary forest typical of the humid zone, whereas much of the lower slopes has been cleared and contains open grassland or secondary forest. The vegetation to the west of the Anosyenne Mountains is distinctly drier and contains a variety of natural habitats, from spiny bush to gallery forest and human-degraded habitats (see Chapters 1 and 2). Generally the slopes along the eastern versant are steeper than those on the western ver-

sant. These different ecological factors have given rise to various types of colonization and life history strategies by different *Simulium* species.

The collections reported on here were carried out within the framework of the project "Biotypologie et biodiversité des eaux continentales malgaches." Given the number of sites visited and the breadth of the collections, it is now possible to estimate the distribution and species richness of several groups of aquatic insects. Here we focus on the inventory and geographic distribution of *Simulium* spp. existing in southeastern Madagascar. All preimaginal forms of *Simulium* are aquatic and restricted to running water. There is considerable variation in this genus in certain life history parameters (e.g., rate of oxygen flow, pH, turbidity, temperature, habitat), and several species are rather strict in their ecological requirements. Furthermore, female *Simulium* are hematophagous and in some cases may be rather dependent on a specific source for blood.

¹ Laboratoire de Recherche sur les Systèmes Aquatiques et leur Environnement, ORSTOM, B.P. 434, Antananarivo (101), Madagascar.

List of *Simulium* Known from Basins in Southeastern Madagascar

Current information on the species diversity of the Malagasy *Simulium* fauna indicates that it is relatively poor in comparison to that of Africa. Thirty-eight species are known from Madagascar, 32 of which have been named, with six currently being described. By comparison, 90 species are known from the African continent. The watersheds of southeastern Madagascar contain 20 species of *Simulium*; this number is exceptionally high in comparison with other areas of the island. Thus, slightly over 50% of the known Malagasy species of this genus occur in the southeast. These species are:

S. adersi Pomeroy, 1921;
S. ambositrae Grenier and Grjébine, 1958;
S. brunhesi Elouard and Ranaivoharindriaka, 1996;
S. gyas de Meillon, 1951;
S. imerinae Roubaud, 1951;
S. impukane de Meillon, 1936;
S. iphias de Meillon, 1951;
S. iphias (10 filaments), undescribed;
S. iphias (15 filaments), undescribed;
S. iphias (17 filaments), undescribed;
S. iphias (18 filaments), undescribed;
S. iphias (19 filaments), undescribed;
S. metecontae Elouard and Pilaka, 1996;
S. neireti Roubaud, 1905;
S. philipponi Elouard and Pilaka, 1997;
S. ruficorne Macquart, 1838;
S. starmuhlneri Grenier and Grjébine, 1963;
S. tolongoinae Grenier, 1972;
S. unicornutum Pomeroy, 1920; and
Simulium new species, undescribed.

Discussion

On the basis of an analysis of the distribution of *Simulium* species known from the basins of southeastern Madagascar, it is possible to distinguish two species groups that correspond to each of the botanical ecosystems.

Group 1

In this group are savannicolous and grassland species that live in tepid, medium- or slow-mov-

ing waters with sandy bottoms. Larvae most often hang or cling to the floating substrates. Species in this group include *Simulium adersi*, *S. ruficorne*, *S. iphias* 15 filaments, *S. iphias* 17 filaments, *S. iphias* 18 filaments, *S. iphias* 19 filaments, *S. imerinae*, *S. philipponi*, *S. impukane*, *Simulium* new species, and *unicornutum* (Fig. 8-1, maps II-V).

Group 2

In this group are forest species that live in fresh waters with relatively rapid currents and occasional waterfalls, and often in rivers that circulate under forest galleries that cover all or nearly all of the river's width. This group includes *Simulium neireti*, *S. ambositrae*, *S. starmuhlneri*, *S. tolongoinae*, *S. iphias* 10 filaments, and *S. gyas* (Fig. 8-1, maps V and VI).

The hydrographic system of the RNI d'Andohahela includes four main basins: the Mandrare (western part), the Tarantsy and the Efaho (southern part), and the Manampanihy (eastern part). Inside the reserve, *Simulium* captured in the upper streams of the Mandrare are different from those recorded in watercourses of the upper part of the Manampanihy. Thus, *S. adersi* and *S. unicornutum* are characteristic of the upper part of the Mandrare Basin, whereas species such as *S. gyas*, *S. starmuhlneri*, *S. tolongoinae*, *S. neireti*, and *S. ambositrae* occur in the upper streams of the Manampanihy Basin.

Simulium starmuhlneri is a strictly forest-dwelling species that has only been found in small tributaries under a continuous covering of forest. Others, such as *S. gyas*, *S. ambositrae*, *S. iphias* 10 filaments, and *S. tolongoinae*, are found in waters that course through a discontinuous forest cover.

Few species occur in microsympatry, and generally one to four species are collected at each site. There is more similarity among the faunas of *Simulium* spp. found in open savannah or grassland habitats than among those from forest habitats. This may be explained by the fact that savannah rivers or those passing through open country are often larger and contain a greater variety of microhabitats within the same system, whereas mountain streams are often smaller and more homogeneous.

Simulium starmuhlneri, *S. tolongoinae*, and *S. neireti* were collected in the forest of the RNI d'Andohahela. None of these *Simulium* are endemic to the reserve, and they are known to occur at other forested sites of eastern Madagascar. This



Map I ● Sampled stations



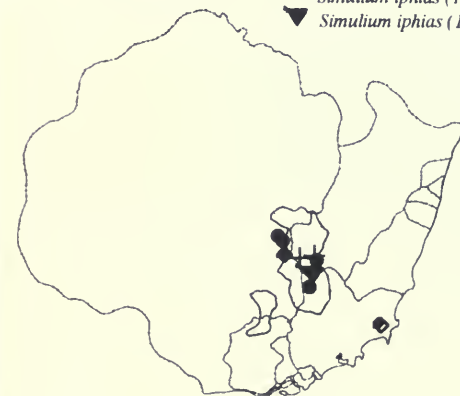
Map II
 ● *Simulium adersi* (17)
 ■ *Simulium ruficorne* (9)
 ▼ *Simulium unicornum* (8)



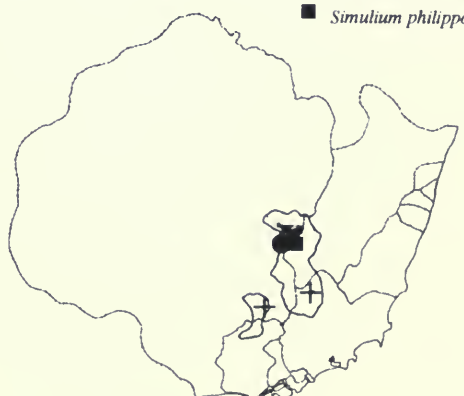
Map III
 ■ *Simulium iphias* (15 fil) (10)
 ● *Simulium iphias* (17 fil) (5)
 ◆ *Simulium iphias* (18 fil) (1)
 ▼ *Simulium iphias* (19 fil) (10)



Map IV
 ● *Simulium brunhesi* (4)
 + *Simulium umerinae* (4)
 ▼ *Simulium metecontae* (1)
 ■ *Simulium philippini* (5)



Map V
 ▼ *Simulium ambositrae* (1)
 ● *Simulium gyas* (4)
 + *Simulium iphias* (10 fil) (1)
 ◆ *Simulium quilleverei* (2)



Map VI
 + *Simulium impukane* (2)
 ● *Simulium neireti* (1)
 ■ *Simulium starmuhlneri* (2)
 ▼ *Simulium tolongoinae* (1)

FIG. 8-1. Maps of the spatial distribution of *Simulium* spp. occurring in southeastern Madagascar. Areas in gray are the parcels of the RNI d'Andohahela. **Map I**, hydrographic network of southeastern Madagascar; **Maps II to VI**, distribution of *Simulium* spp. Key to localities figured on Map II: 1, Mandrare Basin; 2, Manampanihy Basin; 3, Ebakika Basin; 4, Efaho Basin; 5, Tarantsy Basin; 6, small coastal basins; 7 and 8, RNI d'Andohahela.

is in contrast to the tributaries of the Mandrare and the Manampanihy basins, which flow through open zones and from which several new species have been discovered (*S. philipponi*, *Simulium* new species, and *S. brunhesi*).

Acknowledgments

This study represents contribution 13 of the project "Biotypologie et biodiversité des eaux continentales malgaches," run jointly by CNRE and ORSTOM. The program is financed through the French Fonds d'Aide et de Coopération (FAC). We thank our colleagues at Laboratoire de Recherche sur les Systèmes Aquatiques et leur Environnement (LRSAE) for their help and assistance. We are deeply indebted to the Ministère de la Recherche Appliquée au Développement (MRAD) for the facilities made available for our research program. Maps were drawn with the CartoNOE software, written by O. Hertu. S. M. Goodman and two reviewers provided useful comments on an earlier versions of this chapter.

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Chapter 9

Ant Diversity Patterns Along an Elevational Gradient in the Réserve Naturelle Intégrale d'Andohahela, Madagascar

Brian L. Fisher¹

Abstract

Leaf litter ant faunas were inventoried in Madagascar at 430, 800, and 1250 m in parcel 1 of the Réserve Naturelle Intégrale (RNI) d'Andohahela. Within each elevational zone, survey methods involved a combination of pitfall and leaf litter sampling along a 250 m transect. From pitfall and leaf litter samples, I collected and identified 12,285 ants belonging to 25 genera and 111 species; general collecting yielded an additional 28 species.

For each elevation, two species richness estimators—incidence-based coverage estimator (ICE) and first-order jackknife—gave comparable results. Species accumulation curves showed decreased rates of species detection and demonstrated the efficacy of these inventory techniques. Species collected and their relative abundances are presented. Species richness peaked at mid-elevation. Species turnover, complementarity, and faunal similarity measures demonstrated a division in ant communities between lowland forest at ≤ 800 m and montane forest at 1250 m. A mid-elevation peak in species richness is probably the result of the mixing of two distinct, lower and montane forest, ant assemblages.

In addition, I compare complementarity and species turnover values, the number of species restricted to a locality, and the number of species shared between the RNI d'Andohahela, the RNI d'Andringitra, the Réserve Spéciale d'Anjanaharibe-Sud, and the western Masoala Peninsula.

Résumé

Les fourmis de litières ont été inventoriés sur les élévations de 430, 480 et 1250 m dans parcelle 1 de la Réserve Naturelle Intégrale (RNI) d'Andohahela à Madagascar. Pour chaque zone d'élévation, les méthodes d'inventaires utilisées combinent les trous pièges et les échantillonnages de litières le long d'un transect de 250 m.

Avec les trous pièges et les échantillonnages de litières, j'ai pu collecter et identifier 12.285 fourmis appartenant à 111 espèces et 25 genres. Les collections générales ont acquis 28 espèces en plus. Pour chaque élévation, les deux estimateurs de richesse d'espèces telles que l'ICE (Incidence-based coverage estimator) et le premier ordre jackknife ont donnés des résultats comparables. Les courbes d'accumulation d'espèces ont approchées une asymptote et ont montrées l'efficacité de la technique d'inventaires utilisées. Les espèces collectées et leur abondance relatives sont présentées. La richesse d'espèce est au pic à la mid-elevation. Les mesures de la succession continue d'espèces "species turnover," de la complémentarité et de la similarité ont démontrées une division sur la communauté des fourmis entre forets basse de ≤ 800 m et les

¹ Life Sciences Division, South African Museum, P.O. Box 61, 8000 Cape Town, South Africa.

forets de montagnes de 1250 m. Le pic en richesse d'espèces, à la mi-elevation est probablement le résultat de la mixture des fourmis des deux milieux distinctes: fourmis de la foret basse et ceux de la foret de montagne.

En plus, j'ai fait une comparaison entre la RNI d'Andohahela, la RNI d'Andringitra, la Réserve Spéciale d'Anjanaharibe-Sud, et l'Ouest du péninsule de Masoala. La comparaison est basée sur les valeurs de la complémentarité et la succession continue d'espèces "species turnover," le nombre d'espèces unique d'un localité, et le nombre d'espèces communs pour les sites.

Introduction

Geographical patterns of species richness and areas of endemism are two criteria for conservation assessment that require baseline information on species distributions (McNeely et al., 1990). For most invertebrates, we lack this necessary information and even the practical approaches and methods to obtain it. To assign priority to areas with high species richness and endemism in Madagascar, we need methods to inventory the most diverse taxa.

Sampling and estimation procedures for a diverse and ecologically important group of terrestrial insects, ants, were used to assess diversity along elevational gradients in the Réserve Naturelle Intégrale (RNI) d'Andohahela. Similar methods were used to inventory ants in the RNI d'Andringitra (Fisher, 1996a), and in the Réserve Spéciale (RS) d'Anjanaharibe-Sud and on the western Masoala Peninsula (Fisher, 1998). I evaluate the efficacy of the inventory methods and the effect of elevation on species richness in the RNI d'Andohahela. I compare measures of faunal similarity and complementarity for ant species across elevations sampled from 430 to 1250 m. In addition, I compare the ant fauna in the RNI d'Andohahela with those of three other localities and discuss the nature and causes of geographical variation in ant diversity in eastern Madagascar. A complementary aspect of this study is the substantial increase in taxonomic and ecological knowledge of the ant fauna in one of the most threatened regions of the world.

Methods

Study Sites

Surveys were conducted between 12 November and 10 December 1992 near the northern bound-

ary of the RNI d'Andohahela, parcel 1. RNI d'Andohahela comprises 63,100 ha of humid forest within the elevational range of 350–1972 m (Nicoll & Langrand, 1989). Collection sites differed from those during the 1995 inventory discussed elsewhere in this volume. The ant inventory transects were located at: (1) 10 km NW of Enakara, 24°34'S, 46°49'E, transect at 430 m and general collecting from 400 to 450 m; (2) 11 km NW of Enakara, 24°34'S, 46°49'E, transect at 800 m and general collecting from 750 to 850 and 900 to 1000 m; and (3) 13 km NW of Enakara, 24°33'S, 46°48'E, transect at 1,250 m and general collecting from 1180 to 1300 m. Estimated canopy height was 20–30 m at 430 m, 15 m at 800 m, and 6–8 m at 1250 m.

There was no evidence of recent exploitation of the forest at the three transect sites. The transect at 430 m, however, was approximately 200 m from the trail along the northern boundary of the park. The trail was frequently used by local inhabitants for transporting agricultural products and cattle and subsequently showed signs of disturbance.

Survey Methods

In the RNI d'Andohahela, intensive ant surveys were conducted at three sites located at 430, 800, and 1250 m. At each elevation I used 50 pitfall traps and 50 leaf litter samples (mini-Winkler) in parallel lines 10 m apart along a 250 m transect. The site for each transect was chosen with the intent of sampling representative microhabitats found at each elevation (Palmer, 1995). Pitfall traps were placed and leaf litter samples gathered every 5 m along the transect. Pitfall traps consisted of test tubes with an 18 mm internal diameter and 150 mm long, partly filled to a depth of about 50 mm with soapy water and a 5% ethylene glycol solution, inserted into PVC sleeves and buried with the rim flush with the soil surface.

To prevent rainfall from filling the traps, an opaque, ridged piece of plastic was suspended approximately 5 cm above the trap by means of a metal wire support. Traps were left in place for 4 days.

I extracted invertebrates from samples of leaf litter (leaf mold, rotten wood) using a modified form of the Winkler extractor (see Fisher, 1996a, Fig. 8-1, and Fisher, 1998, Fig. 4-1). The leaf litter samples involved establishing 50 1 m² plots separated by 5 m along the transect line. The leaf litter inside each plot was collected and sifted through a wire sieve of 1 cm grid size. Before sifting, the leaf litter material was minced using a machete to disturb ant nests in small twigs and decayed logs. Approximately 2 liters of sifted litter was taken from each 1 m² plot. At the low elevations (<800 m) litter was occasionally sparse, and sometimes less than 2 liters was taken. If the subsample plot contained a large rotten log or thick litter, 2 liters of litter was the maximum amount taken at each subsample site. This 2 liter limit was imposed because of the size of the Winkler extractor. In those sites where 1 m² provided an excess of leaf litter, the plot was subsampled until 2 liters of litter was obtained. Ants and other invertebrates were extracted from the sifted litter during a 48 hr period in mini-Winkler sacks (for a detailed discussion of the mini-Winkler method, see Fisher, 1996a, 1998).

I also surveyed ants through general collecting, defined as any collection that was separate from the mini-Winkler or pitfall transects, including searching in rotten logs and stumps, in dead and live branches, in bamboo, on low vegetation, under canopy moss and epiphytes, under stones, and leaf litter sifting. At each transect site, general collections were conducted for an approximately 2-day period. General collections were made within 500 m ground distance and within 75 m in elevation of each transect site. In addition, general collecting was conducted between 900 and 1000 m. General collections included samples of the arboreal ants found on low vegetation that were not sampled by pitfalls or leaf litter. Ants sampled with general collection methods, therefore, were not used in the analysis of the efficacy of the survey of the leaf litter ants, of faunal similarity, or complementarity.

Sample Processing

For every 50-station transect, which took from 5 to 7 field days to conduct, an average of 1

month was spent in the laboratory sorting, identifying, and curating specimens. After I returned from the field, ant specimens from the pitfall and leaf litter samples were sorted. The saturated salt water extraction procedure described below was very effective in removing organic matter from inorganic matter in the leaf litter samples. Each sample was emptied into a 40 mm diameter, 250 ml graduated cylinder. A near boiling saturated salt water solution was then added until the cylinder was half filled. After 2 minutes the solution was stirred. After settling for about 2 minutes the organic matter was decanted off the top into a strainer and rinsed with water, then with 95% ethanol. This process was repeated two to three times for each sample. The residue at the bottom of the cylinder was checked for large arthropods that were too heavy to float to the top of the cylinder.

Next, each sample was sorted by genus. Trained student assistants (parataxonomists *sensu* Wheeler, 1995) sorted and identified all material down to the genus level. All ant specimens from a single genus were then sorted to species by me, by examining specimens sequentially from each elevational site. This method allowed the greatest number of specimens within an elevational site to be identified while in alcohol and thus limited the cost in time of mounting specimens. Data for specimens were managed using Biota (Colwell, 1996).

Identification

Specimens were identified to morphospecies by me, based on characters previously established to be important at the species level for each genus. When possible, species names were attached to these morphospecies by using taxonomic descriptions (see Fisher, 1997, for a list of references) and by comparing specimens with those previously collected by P. S. Ward and me in Madagascar that had been compared to type material. Species codes used in this paper correspond to species codes used in Fisher (1996a, 1998). A representative set of specimens will be deposited at the Museum of Comparative Zoology at Harvard University and in Madagascar.

Data Analysis

EVALUATION OF SAMPLING METHOD—To assess survey completeness for the elevations sampled,

TABLE 9-1. Ant species list for the RNI d'Andohahela, including elevation and collection method.

Genus	Species	430 m	800 m	900-1000 m	1250 m
CERAPACHYINAE					
<i>Cerapachys</i>	2		W		
	3		W, G	G	
	4				G
	5		W		W
	6		P		
	7				W
	8		W		W, G
	2	G			
Sinopone					
FORMICINAE					
CAMPONOTINI					
<i>Camponotus</i>	2				G
	5	G			P
	6		W, P, G		
	7				G
	8				G
	9				G
	10		G		G
	12				W, G
	15		W, G		
	23				G
	24				P
	28				W
	<i>hildebrandti</i>	G			
LASIINI					
<i>Paratrechina</i>	1	W, P, G	W, P, G		W, P, G
	4				W
	5	W, P, G	W, P, G	G	W, G
	6	W	W		W
PLAGIOLEPIDINI					
<i>Plagiolepis</i>	2				G
	3	W	W		W
MYRMICINAE					
CREMATOGASTRINI					
<i>Crematogaster</i>	3	W	W		
	4				G
	11	W	W		W, G
	<i>schenki</i>				W, P, G
DACETONINI					
<i>Kyidris</i>	1	W	W		
	2				W, G
	3		G		
<i>Smithistruma</i>	1		W, P		W
	2				W
	3				
	13	G			
	14	W	P		
	16	W	W		W
	18	W, G	W		W, G
	20	W	W		
	21				W
	51		W		
	<i>grandidieri</i>				W, G

TABLE 9-1. Continued

Genus	Species	430 m	800 m	900-1000 m	1250 m
PHALACROMYRMECINI					
<i>Pilotrochus</i>	<i>besmerus</i>				W, G
PHEIDOLINI					
<i>Aphaenogaster</i>	1				G
<i>Pheidole</i>	6		W, P		W, G
	7	W, P, G	W		
	8				W, P, G
	10	W, P	W, P		W, P
	11	P			W, G
	13		W		
	14	W, P	W, P, G		
	17			G	
	23	P, G	W, P		W
	24				W
	25	W, P	P		
	26		W		
	27	W	W, P		
	28	W, P, G	P		
	29	W, P			
	31			G	W, P
	32	W			
	33	W			
	34				G
	35	W			W
	38	W			
	<i>longispinosa</i>	W, P, G	W, P, G		W
	<i>nemoralis</i>	W, P	W, P		
	<i>veteratrix</i>	W, P, G	W, P, G	G	W, P
PHEIDOLOGETONINI					
<i>Oligomyrmex</i>	3	W			
	6	W	W		
SOLENOPSIDINI					
<i>Monomorium</i>	5	W, G	W		W
	7	W	W		
	14	W			
	17				P
	18	W	W		
	19				W
	20				W, P
	21		W		
	22				W
	25		W		W, P, G
	43	G			
TETRAMORIINI					
<i>Tetramorium</i>	6	G	W, P	G	W, P, G
	13		P		P
	14				W, P
	15				P
	16	W, P			
	18	W	W, P		W, P, G
	19	G			
	20		W, G		
	22	W	W, P		
	23	W, P	P		
	27	W, G	W		
	30	G			
	31		W, G		W
	32				G
	33		W, P		W, G
	<i>dysalum</i>		W, P		
	<i>electrum</i>	W, P	W, P		

TABLE 9-1. *Continued*

Genus	Species	430 m	800 m	900-1000 m	1250 m
INCERTAE SEDIS					
Undescribed genus	1		W	G	
PONERINAE					
AMBLYOPONINI					
<i>Amblyopone</i>	1		W		
	2				W, G
	3				W
<i>Mystrium</i>	1	W	W		
	2	G		G	
<i>Prionopelta</i>	2	W			
	4		W		
ECTATOMMINI					
<i>Discothyrea</i>	1				W, G
<i>Proceratium</i>	1		W		
PLATYTHYREINI					
<i>Platythyrea</i>	<i>bicuspis</i>		P		
PONERINI					
<i>Anochetus</i>	<i>grandidieri</i>	W	W, P, G		
<i>Hypoponera</i>	1		W		W, P, G
	4	G			W
	5		W		
	6	W	W		
	7		W		W, G
	8				W, G
	9		W		W
	11		W		W, G
	12		W		
	13		W		
	14	G			
	16	W			
	18		W		
	<i>sakalava</i>	G		G	W, G
<i>Leptogenys</i>	1			G	P, G
	2	P	P		W, P, G
	4				W
<i>Pachycondyla</i>	<i>cambouei</i>	W, P, G	W, P, G	G	W, P, G
	<i>sikorae</i>	G		G	
PSEUDOMYRMECINAE					
<i>Tetraponera</i>	<i>grandidieri</i>	W, G	W, P		
	<i>hysterica</i>	G			
	psw-70		G		
	psw-81	W	W, P		
	psw-92	G			
Total species: G		27	15	12	39
Total species: P		18	30		20
Total species: W		46	63		53
Total species: W and P		49	71		59
Total species: all methods		64	74		71
Number (%) of unique species: all methods		18 (28%)	20 (27%)	1 (8%)	35 (49%)
Number (%) of unique species: W and P		9 (18%)	20 (28%)		29 (49%)
Total number of G collections		40	12	12	23
Number of workers: G		814	172	98	348
Number of workers: P		852	1,038		430
Number of workers: W		4,032	3,679		2,254
Total number of workers		5,698	4,889		3,032
Abundance: total number stations collected		519	641		528

Notes: Only collections of workers are presented (G = from general collections; P = from pitfall transect samples; W = from mini-Winkler, leaf litter transect samples). A total of 137 ant species and 13,717 workers were collected. In addition, *Cardiocondyla emeryi* and *Eutetramorium* sp. 1 from 1250 m were recorded from queens only. Abundance refers to the total number of stations where each species was collected.

I plotted species accumulation curves for each elevation. Species accumulation was plotted as a function of the number of leaf litter and pitfall trap samples taken. For the analysis, each leaf litter sample was paired with the adjacent pitfall sample, collectively termed a station sample. Species accumulation curves for the 50 stations per transect, as well as incidence-based coverage estimator (ICE) and first-order jackknife estimates of the total number of species in the local community from which the samples were taken, were plotted for each succeeding station sample. ICE and the first-order jackknife methods are nonparametric approaches to improving the estimate of species richness. ICE is based on species found in 10 or fewer sampling units (Lee & Chao, 1994; Chazdon et al., 1998). Standard deviations of ICE are based on bootstrap estimates (Colwell, 1997). The first-order jackknife is based on the observed frequency of unique species at a 50-station transect. The jackknife estimator and its standard deviation are defined in Heltshe and Forrester (1983). For species accumulation curves, sample order was randomized 100 times, and the means and standard deviations of ICE and the jackknife estimates were computed for each succeeding station using the program EstimateS (Colwell, 1997; see also Colwell & Coddington, 1994; Chazdon et al., 1998).

ANT DIVERSITY—Data on both species richness and abundance were used to assess the change in species composition along the elevational gradient. Only records of ant workers were used in these calculations. Because alates may travel considerable distances during dispersal, their presence does not necessarily signify the establishment of a colony of that species within the transect zone. In addition, collections of queens and males dispersing from nearby nests at the time of the survey may bias the relative abundance of the species. Because ants are colonial, abundance measures were not based on the total number of individual workers collected at each transect site, but rather on species frequency defined as the proportion of stations, out of 50, in which each species was collected at a site.

For each elevation, I compared ICE and first-order jackknife estimates of total species richness and their 95% confidence limits. Overlap and complementarily (distinctness or dissimilarity *sensu* Colwell & Coddington, 1994) of the ant assemblages at different elevations were assessed using distance, faunal similarity, and beta-diversity indices. The proportion of all species in two

sites that occurred in only one or the other was calculated using the Marczewski-Steinhaus (M-S) distance index based on presence/absence data: $C_{MS} = (a + b - 2j)/(a + b - j)$, where j = number of species found at both elevations, a = number of species at elevation A, and b = number of species at elevation B (Pielou, 1984; Colwell & Coddington, 1994). Similarity of the ant fauna was assessed using the simplified Morisita Index, which incorporates abundance data:

$$C_{MH} = \frac{2 \sum (a_i \times b_i)}{(da + db)aN \times bN},$$

where

$$da = \frac{\sum a_i^2}{aN^2} \quad \text{and} \quad db = \frac{\sum b_i^2}{bN^2},$$

aN = total number of station/species occurrences in elevation A, bN = total number of station/species occurrences in elevation B, a_i = the number of stations occupied by the i th species in elevation A, and b_i = the number of stations occupied by the i th species in elevation B (Horn, 1966; Wolda, 1981). Indices based on presence/absence data have been shown to be strongly influenced by species richness and sample size (Wolda, 1981). The Morisita Index is nearly independent of species richness and sample size (Wolda, 1981) and may therefore be more appropriate for comparisons of ant assemblages between sites along an elevational gradient that differ greatly in species richness.

Beta-diversity (species turnover between elevations) was calculated in two ways. First, the beta-diversity measure of Whittaker (1960) was used: $\text{Beta-1} = (S/a) - 1$, where S = the total number of species in the two elevations combined and a = the mean number of species in each elevation. Because this measure does not distinguish between species turnover and the loss of species along a gradient without adding new species, the measure of beta-diversity developed by Harrison et al. (1992) was also calculated: $\text{beta-2} = (S/a_{\max}) - 1$, where S is the same as beta-1 above and a_{\max} = the maximum value of alpha-diversity (i.e., number of species) among the elevations compared. The number of species unique to an elevation and the number of species shared between elevations were also compared.

In addition, I also calculated complementarity, species turnover, number of unique species, and number of species shared among the RNI d'Andohahela and three other localities surveyed using the same methods: the RNI d'Andringitra,

TABLE 9-2. Abundance measured as frequency of occurrence (proportion of stations out of 50 paired pitfall and leaf litter samples at which each species was recorded) for each elevation in the RNI d'Andohahela.

Genus	Species	430 m	800 m	1250 m
CERAPACHYINAE				
<i>Cerapachys</i>	2		0.04 (5)	
	3		0.06 (10)	
	5		0.02 (1)	0.06 (9)
	6		0.02 (1)	
	7			0.08 (4)
	8		0.04 (5)	0.08 (5)
FORMICINAE				
CAMPONOTINI				
<i>Camponotus</i>	5			0.02 (1)
	6		0.04 (2)	
	12			0.06 (126)
	15		0.02 (1)	
	24			0.02 (1)
	28			0.08 (4)
LASIINI				
<i>Paratrechina</i>	1	1.00 (2,090)	0.32 (103)	0.36 (112)
	4			0.10 (42)
	5	0.48 (254)	0.44 (754)	0.04 (29)
	6	0.02 (2)	0.06 (6)	0.02 (1)
PLAGIOLEPIDINI				
<i>Plagiolepis</i>	3	0.02 (1)	0.08 (8)	0.42 (112)
MYRMICINAE				
CREMATOGASTRINI				
<i>Crematogaster</i>	3	0.02 (1)	0.02 (1)	
	11	0.08 (6)	0.04 (4)	0.28 (17)
	<i>schenki</i>			0.72 (166)
DACETONINI				
<i>Kyidris</i>	1	0.04 (6)	0.02 (1)	
<i>Smithistruma</i>	2			0.06 (4)
<i>Strumigenys</i>	1		0.90 (989)	0.02 (1)
	2			0.04 (13)
	13	0.04 (4)	0.02 (1)	
	14	0.14 (8)	0.32 (38)	
	16	0.04 (4)	0.02 (1)	0.04 (6)
	18	0.42 (39)	0.20 (41)	0.62 (113)
	20	0.04 (3)	0.10 (8)	
	21			0.08 (6)
	51		0.02 (1)	
	<i>grandidieri</i>			0.02 (2)
PHALACROMYRMECINI				
<i>Pilotrochus</i>	<i>besmerus</i>			0.08 (4)
PHEIDOLINI				
<i>Pheidole</i>	6		0.24 (75)	0.02 (3)
	7	0.38 (133)	0.28 (82)	
	8			0.74 (332)
	10	0.04 (2)	0.12 (28)	0.48 (76)
	11	0.04 (12)		0.04 (2)
	13		0.02 (1)	
	14	0.14 (16)	0.44 (178)	
	23	0.12 (95)	0.12 (26)	0.02 (1)
	24			0.02 (1)
	25	0.54 (110)	0.16 (48)	

TABLE 9-2. *Continued*

Genus	Species	430 m	800 m	1250 m
	26		0.36 (110)	
	27	0.36 (72)	0.32 (120)	
	28	0.90 (224)	0.02 (1)	
	29	0.12 (72)		
	31			0.06 (11)
	32	0.02 (1)		
	33	0.02 (1)		
	35	0.02 (1)		0.04 (8)
	38	0.02 (3)		
	<i>longispinosa</i>	0.98 (1,010)	0.68 (510)	0.04 (2)
	<i>memoralis</i>	0.28 (78)	0.32 (76)	
	<i>veteratrix</i>	0.24 (80)	0.52 (218)	0.38 (107)
PHEIDOLOGETONINI				
<i>Oligomyrmex</i>	3	0.02 (1)		
	6	0.10 (6)	0.14 (37)	
SOLENOPSIDINI				
<i>Monomorium</i>	5	0.50 (67)	0.40 (57)	0.34 (142)
	7	0.02 (3)	0.10 (69)	
	14	0.16 (28)		
	17			0.02 (1)
	18	0.30 (108)	0.48 (81)	
	19			0.02 (2)
	20			0.18 (48)
	21		0.02 (3)	
	22			0.10 (98)
	25		0.10 (7)	0.04 (3)
TETRAMORIINI				
<i>Tetramorium</i>	6		0.18 (21)	0.10 (8)
	13		0.02 (1)	0.02 (5)
	14			0.20 (39)
	15			0.02 (1)
	16	0.24 (37)		
	18	0.02 (1)	0.80 (253)	0.52 (109)
	20		0.18 (18)	
	22	0.02 (4)	0.12 (17)	
	23	0.14 (19)	0.02 (1)	
	27	0.02 (1)	0.02 (1)	
	31		0.06 (3)	0.06 (5)
	33		0.14 (9)	0.30 (43)
	<i>dysalum</i>		0.30 (151)	
	<i>electrum</i>	0.26 (76)	0.18 (28)	
INCERTAE SEDIS				
Undescribed genus	1		0.02 (1)	
PONERINAE				
AMBLYOPONINI				
<i>Amblyopone</i>	1		0.06 (8)	
	2			0.12 (10)
	3			0.08 (5)
<i>Mystrium</i>	1	0.10 (5)	0.02 (1)	
<i>Prionopelta</i>	2	0.14 (9)		
	4		0.16 (18)	
ECTATOMMINI				
<i>Discothyrea</i>	1			0.10 (6)
<i>Proceratium</i>	1		0.02 (1)	

TABLE 9-2. *Continued*

Genus	Species	430 m	800 m	1250 m
PLATYTHYREINI				
<i>Platythyrea</i>	<i>bicuspis</i>		0.02 (1)	
PONERINI				
<i>Anochetus</i>	<i>grandidieri</i>	0.40 (35)	0.20 (27)	
<i>Hypoponera</i>	1		0.06 (14)	0.82 (389)
	4			0.02 (8)
	5		0.02 (1)	
	6	0.50 (71)	0.24 (86)	
	7		0.18 (11)	0.38 (42)
	8			0.16 (18)
	9		0.10 (6)	0.08 (14)
	11		0.46 (56)	0.66 (232)
	12		0.02 (1)	
	13		0.36 (33)	
	16	0.02 (2)		
	18		0.06 (5)	
	<i>sakalava</i>			0.34 (42)
<i>Leptogenys</i>	1			0.02 (2)
	2	0.08 (4)	0.16 (10)	0.34 (33)
	4			0.02 (1)
<i>Pachycondyla</i>	<i>cambouei</i>	0.68 (72)	0.90 (221)	0.36 (56)
PSEUDOMYRMECINAE				
<i>Tetraponera</i>	<i>grandidieri</i>	0.04 (4)	0.04 (2)	
	psw-81	0.06 (3)	0.06 (3)	

The number of individual workers collected is given in parentheses.

the RS d'Anjanaharibe-Sud, and the western Ma-soala Peninsula.

Results

In the RNI d'Andohahela I collected and identified 13,717 ants comprising 29 genera and 139 species from general collections, leaf litter, and pitfall methods. These included 155 queens and 86 males. Leaf litter and pitfall methods yielded 12,285 worker ants belonging to 25 genera and 111 species. A list of ant species from this study in the RNI d'Andohahela based on all collecting methods and separated by elevation and technique is presented (Table 9-1). General collections from 900 to 1000 m are also presented. Absent from Table 9-1 are records of species known from queens only: *Cardiocondyla emeryi* and *Eutetramorium* sp. 1, both from 1250 m.

Within the RNI d'Andohahela, the 800 m zone had the greatest total number of species recorded (74 species total from all methods; 71 species total from litter and pitfall samples; Table 9-1). The same relative ranking in observed species richness

between sites was reached and maintained after three station samples (Table 9-5). The numbers of species and individuals collected from pitfall traps were low compared to those collected by mini-Winkler methods. Only six species that were collected by pitfall traps were not also collected by the mini-Winkler method. In a study using comparable methods in dry forest in southwestern Madagascar, however, pitfall traps collected a greater proportion of individuals and species (Fisher & Razafimandimby, 1997).

The abundance of ant species is presented in Table 9-2. Both the proportion of stations at which each species was collected and the number of individuals collected are given. General collections are not included. Only 15 species out of 111 (14%) were found at all three elevations. The relative frequencies of occurrence of these species, however, often differed considerably from one site to the next. For example, *Paratrechina* sp. 5 had relative frequencies of 0.48 at 430 m, 0.44 at 800 m, and 0.04 at 1250 m (Table 9-2). Thirty-eight species (34%) were collected at two of the three elevational sites.

The number of ant species and their abundance, measured as the total number of stations where

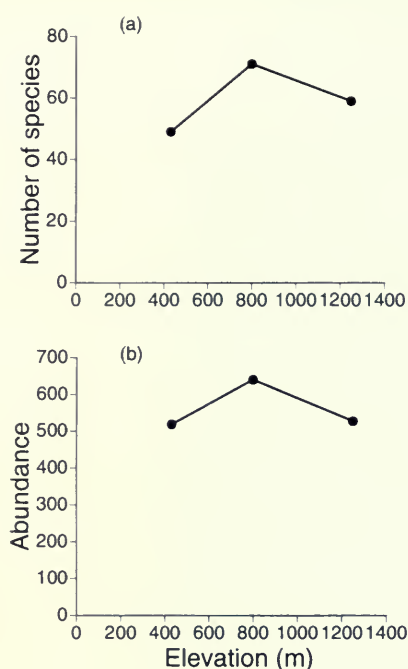


FIG. 9-1. The number of ant species (a), and the total abundance (b) as a function of elevation. Abundance is measured as the total number of stations where each species was collected (see text for details). Data are from pitfall and mini-Winkler samples.

each species was collected, peaked at 800 m (Fig. 9-1). The relative prevalence of each subfamily for the combined pitfall and leaf litter samples for each elevation and for all elevations is shown in Table 9-3. The fauna was dominated by Myrmicinae in both numbers of species and individuals, followed by Ponerinae. The ratio of Ponerinae to Myrmicinae was similar at 800 and 1250 m (0.41 and 0.42, respectively), but was lower at 430 m (0.19).

Observed number of species, ICE, and first-order jackknife estimates of species richness, their standard deviation, and 95% confidence intervals are presented for the RNI d'Andohahela (Table 9-

4). Observed species richness for each elevation surveyed in the RNI d'Andohahela, evaluated at different sample sizes, is presented in Table 9-5. Species accumulation curves for observed, ICE, and jackknife estimates showed a decrease in the rate of species accumulation, but were still increasing slowly (Fig. 9-2). In a combined analysis of the three elevations in the RNI d'Andohahela, the pitfall and mini-Winkler methods collected 86% of the total number of leaf litter ant species estimated by ICE that could be collected using these methods in the transect areas (Fig. 9-2d).

The greatest dissimilarity (M-S Index) and lowest similarity (simplified Morisita Index) values between adjacent elevations occurred between 800 and 1250 m (Table 9-6). Similarly, the greatest species turnover (beta-diversity) occurred between 800 and 1250 m (Table 9-7). The overall beta-1 and beta-2 values of species turnover between all elevations were 0.860 and 0.563, respectively.

The 1250 m site had the greatest number and the highest percentage of species restricted to one specific elevation (Table 9-1). The 800 m site had the highest number of species shared with other sites (Table 9-6). The 800 m site shared more species with the 1250 m site than with the 430 m site (Table 9-6).

The ant fauna at the RNI d'Andohahela was compared to the fauna at three other localities where similar inventories have been conducted. The elevations surveyed at all four localities are presented in Table 9-8, and their distances apart (km) are presented in Table 9-9. The matrix of complementarity values shows a high level of distinctness between localities (Table 9-10). The ant faunas of the RNI d'Andohahela and the RNI d'Andringitra (65% distinct; 275 km apart), and between the RS d'Anjanaharibe-Sud and the western Masoala Peninsula (72% distinct; 110 km apart) show the lowest level of distinctness. The RNI d'Andringitra and the RS d'Anjanaharibe-Sud (87% distinct; 900 km apart) and the RNI

TABLE 9-3. Total number and percentage (%) of species of each subfamily for pitfall and leaf litter collections on the RNI d'Andohahela (general collections are excluded). P/M refers to the taxonomic ratio of species in the Ponerinae and Myrmicinae. Subfamily names are abbreviated (see Table 9-1).

Elevation (m)	Cerap	Form	Pon	Myrm	Pseudo	P/M
430	0	4 (8%)	7 (14%)	36 (74%)	2 (4%)	0.19
800	5 (7%)	6 (8%)	17 (24%)	41 (58%)	2 (3%)	0.41
1250	3 (5%)	9 (15%)	14 (24%)	33 (56%)	0	0.42
All elevations	6 (5%)	11 (10%)	27 (24%)	65 (59%)	2 (2%)	0.41

TABLE 9-4. The number of species collected, incidence-based coverage estimator (ICE), and first-order jackknife estimates of total species richness (with 95% confidence intervals, CI), based on pitfall and leaf litter transects in the RNI d'Andohahela. Statistics are given for each altitude and for all elevations combined.

Elevation (m)	Observed	ICE	95% CI	Jack-knife	95% CI
430	49	61.7	0.32	61.7	0.61
800	71	90.3	0.28	90.6	0.79
1250	59	72.0	0.31	73.7	0.70
All elevations	111	129.4	0.11	135.8	0.20

d'Andohahela and the western Masoala Peninsula (87% distinct; 845 km apart) had the greatest complementarity. Species turnover values show the same pattern (Table 9-10). In a comparison of all 800 m zone sites (Table 9-11) and all 1200 m

TABLE 9-5. Observed species richness for each elevation surveyed in the RNI d'Andohahela, evaluated at different sample sizes. Richness values are the means of 100 randomizations of sample accumulation order. Standard deviations are given in parentheses.

Stations sampled	430 m	800 m	1250 m
1	10.7 (2.90)	12.7 (4.01)	10.8 (2.53)
3	18.8 (3.19)	25.5 (4.09)	20.8 (2.69)
5	23.5 (3.01)	33.6 (3.81)	26.7 (2.72)
10	30.6 (2.49)	44.4 (3.09)	35.3 (2.91)
15	34.7 (1.95)	50.6 (3.06)	41.2 (2.94)
20	37.7 (1.96)	55.2 (2.70)	45.5 (2.84)
25	40.4 (1.84)	68.7 (2.52)	48.8 (2.73)
30	42.5 (1.77)	61.7 (2.35)	51.3 (2.30)
35	44.4 (1.51)	64.4 (2.25)	53.8 (2.07)
40	46.2 (1.28)	66.8 (1.78)	55.8 (1.57)
45	47.7 (0.98)	69.0 (1.18)	57.5 (1.19)
50	49	71	59

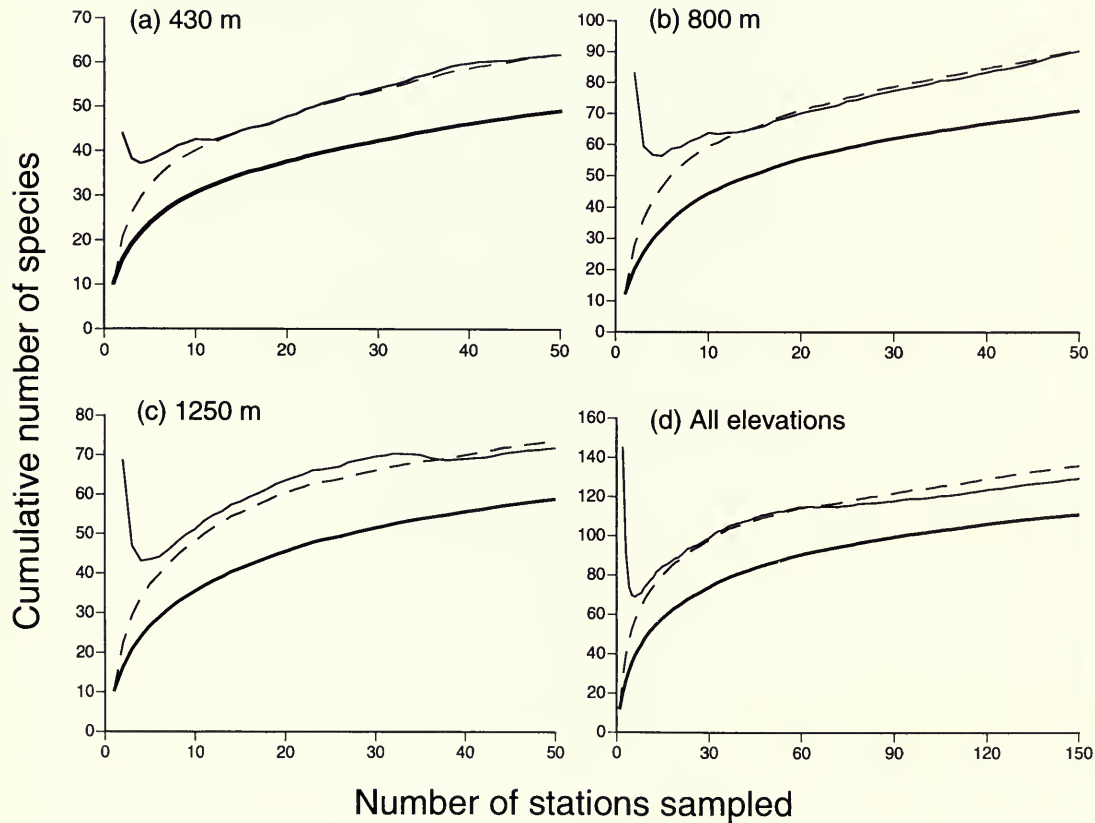


FIG. 9-2. Assessment of leaf litter ant sampling technique for each elevation (a–c) and for all elevations combined (d) in the RNI d'Andohahela. The lower species accumulation curve (*thick line*) in each chart plots the observed number of species as a function of the number of stations sampled. The upper curves display the nonparametric first-order jackknife (*dashed line*) and incidence-based coverage estimator (ICE) (*solid line*) estimated total species richness based on successively larger numbers of samples from the data set (Heltsh & Forrester, 1983; Lee & Chao, 1994). Curves are plotted from the means of 100 randomizations of sample accumulation order.

TABLE 9-6. Complementarity and faunal similarity between the three elevational zones sampled in the RNI d'Andohahela. Above the diagonal is the Marczewski-Steinhaus (M-S) distance index (presence/absence data; Pielou, 1984) and below the diagonal, simplified Morisita index of similarity (abundance data; Horn, 1966). Higher values represent greater distinctness (M-S) or similarity (Morisita). Bold values represent comparisons of altitudinally adjacent transects. The number of species shared between elevations is presented in parentheses above the diagonal.

Elevation	430 m	800 m	1250 m
430 m	—	0.537 (38)	0.813 (17)
800 m	0.584	—	0.725 (28)
1250 m	0.257	0.411	—

zone sites (Table 9-12), the same pattern of complementarity and species turnover values were found. In Table 9-11, data from the 785 and 825 m sites in the RNI d'Andringitra (see Table 9-8) were combined. The same pattern was obtained when the 785 or 825 m sites were analyzed separately with the balance of the 800 m zone sites from the other localities.

Discussion

The RNI d'Andohahela Ant Fauna

We are far from the saturation point in our efforts to discover undescribed ant species in Madagascar. In terms of numbers of new species collected per site inventoried, we are still on the steep part of the curve. There may be 1,000 species on the island, with two-thirds of the species undescribed (Fisher, 1996b, 1997). No previous records exist for ants collected in the RNI d'Andohahela. Subsequent collections of ants in other parts of the RNI d'Andohahela region have been made by P. S. Ward, G. D. Alpert, and K. C. Emberton, and they reveal additional species diversity within the region not recorded during this 1992 survey.

For the island of Madagascar, 90% of the valid specific and subspecific ant taxa are endemic (Fisher, 1996b, 1997). In the RNI d'Andohahela, nearly 100% of the ants collected are thought to be endemic to Madagascar, except for *Cardiocondyla emeryi*, which is a pantropical tramp species and is known throughout the Malagasy region (Bolton, 1982; Fisher, 1997).

TABLE 9-7. Beta-1 (above the diagonal) and beta-2 (below the diagonal) diversity values of each pair of altitude sites in the RNI d'Andohahela. Higher values represent greater species turnover. Bold values represent comparisons of altitudinally adjacent transects. Overall beta-1 diversity was 0.860 and that of beta-2 was 0.563.

Elevation	430 m	800 m	1250 m
430 m	—	0.366	0.685
800 m	0.155	—	0.569
1250 m	0.542	0.437	—

Many interesting and rare taxa were collected at the 1250 m site. For example, a single worker of *Aphaenogaster* sp. 1 was collected in a general collection from the leaf litter. This is the first record from the southern half of the island of a montane forest *Aphaenogaster*. At the 1250 m site, seven workers and two queens of *Pilotochus besmerus* were collected; this is the second record of this endemic Malagasy monotypic genus. *Pilotochus* was previously known only from a single worker collected in a Berlese sample along the road to Anosibé An'Ala, 33 km south of Moramanga, in east central Madagascar in 1975 (Brown, 1978). The generic name is derived from the Greek *pilos* (hair) + *trochos* (wheel), in reference to its amazing mesopleural "hair-organ."

In addition, other rare species and genera collected at the 1250 m site include two species of *Amblyopone*, one species each of *Smithistruma*, *Discothyrea*, *Eutetramorium*, and an undescribed myrmicine genus. Previously, *Eutetramorium* was thought to be endemic to the dry and eastern humid forests of the northern half of Madagascar. At the 1250 m site, a queen of *Eutetramorium* sp. 1 was collected in a leaf litter sample. In 1993, P. S. Ward collected a single worker-queen intermediate in a Winkler sample in humid forest at 1050 m in the RNI d'Andohahela, 3 km east of Mahamavo. This suggests that although queens and worker-queen intermediates may be found in the leaf litter, the nest is located elsewhere, in the canopy or in fallen hard wood that is not sampled by the leaf litter technique. Fallen trees with hard wood are a microhabitat that is often overlooked by ant collectors.

The undescribed myrmicine genus was thought to be endemic to the humid forest of northeastern Madagascar (Fisher, 1998). In the RNI d'Andohahela, a different species of the undescribed genus of myrmicine was collected in a large rotten log at 950 m and in a leaf litter sample

TABLE 9-8. Elevations surveyed within each elevational zone in the RNI d'Andohahela, the RNI d'Andringitra, the RS d'Anjanaharibe-Sud, and on the western Masoala Peninsula.

Location	0 m	400 m	800 m	1200 m	1600 m	2000 m
Andohahela		430	800	1250		
Andringitra			785, 825	1275	1680	
Anjanaharibe-Sud			875	1200	1565	1985
Masoala	25	425	825			

at 800 m. These records of *Pilotrochus*, *Eutetramorium* and the undescribed genus suggest that the geographical ranges of these genera may extend patchily across the entire length of the eastern humid forest.

Elevational Gradient and Complementarity

Faunal similarity, distinctness, and species turnover measures (Tables 9-5 and 9-7) support a division of the ant fauna into two assemblages, one occurring in lowland forests ≤800 m and the other in montane forests at 1250 m. Between adjacent sites, species turnover was greater between 800 and 1250 m than between 430 and 800 m. In previous studies in the RNI d'Andringitra (Fisher, 1996a), and in the RS d'Anjanaharibe-Sud and on the western Masoala Peninsula (Fisher, 1998), mid-elevation sites (ca. 800 m) had the highest rate of species turnover.

Species richness did not decrease monotonically as a function of elevation (Fig. 9-1). A mid-elevation peak has been documented for ants in Madagascar (Fisher, 1996a, 1998), in Panama (Olson, 1994), and for other taxa (Rahbek, 1995). The mid-elevation peak observed in ant species richness in Madagascar may be the result of a mixing of two distinct ant assemblages along an ecotone.

As suggested in Fisher (1998) for the ant fauna in the RS d'Anjanaharibe-Sud and on the western

Masoala Peninsula, species richness may increase from low elevation (430 m) to mid-elevation (800 m) because the 800 m site is adjacent to the source-pool of the distinct montane ant fauna as well as those from lower elevations. The proximity of elevational zones encourages the establishment of marginal populations from adjacent elevations (Pulliam, 1988; Stevens, 1989, 1992; Rahbek, 1997). A mixing of the lowland and montane ant assemblages results in the peak in species richness. In the RNI d'Andohahela, the mid-elevation site (800 m) has the highest number of species shared with other sites: 38 species with 430 m and 28 species with 1250 m (Table 9-6). The number of species shared by the lowest elevation site decreases with increasing change in elevation.

An alternative hypothesis to that of the mixing of lowland and montane ant assemblages is that mid-elevations provide the most "suitable" environment for ants (Rosenzweig & Abramsky, 1993). This assumes that the suitable environment favors an increase in species richness rather than an increase in the population numbers of species. There is currently no accepted explanation of why the most suitable habitats would occur at mid-elevations or how these habitats would increase species richness (Rosenzweig & Abramsky, 1993; Rahbek, 1997).

Efficacy of Inventory Methods

The efficacy of the inventory methods can be evaluated by using species accumulation curves (Colwell & Coddington, 1994). The criterion I use to evaluate efficacy is the number of species collected per unit effort. For every 50-station transect, which takes an average of 7 field days to conduct, 1 month must be spent in the laboratory sorting, identifying, and curating specimens. If increased sampling efforts always collect additional species, how many subsamples should be taken?

An accumulation curve is specific to the area

TABLE 9-9. Distance (km) between the RNI d'Andohahela, the RNI d'Andringitra, the RS d'Anjanaharibe-Sud, and the western Masoala Peninsula.

	Andohahela	Andringitra	Anjanaharibe-Sud
Andringitra	275	900	110
Anjanaharibe-Sud		845	
Masoala	1,170	1,200	

TABLE 9-10. Complementarity (M-S, above the diagonal) and beta-1 (below the diagonal) diversity values between the RNI d'Andohahela, the RNI d'Andringitra, the RS d'Anjanaharibe-Sud, and the western Masoala Peninsula. The number (percentage) of species specific to the locality are presented along the diagonal. Total number of species for all localities is 381.

	Andohahela	Andringitra	Anjanaharibe-Sud	Masoala
Andohahela	37 (33)	0.647	0.850	0.846
Andringitra	0.478	45 (39)	0.874	0.872
Anjanaharibe-Sud	0.739	0.776	79 (44)	0.720
Masoala	0.734	0.773	0.562	78 (47)

of the survey, the season or year, and the collecting techniques employed. Additional collecting methods, or a survey in a different area or season at the same elevation, would most likely collect additional species. If an observed or estimated species accumulation curve demonstrates a sufficient decrease in the rate of species accumulation, then the number of subsamples is arguably adequate for collecting the species in the area surveyed for the particular methods employed. Conversely, if the curves are rising rapidly, more intensive sampling may be necessary to accurately compare diversities between elevations. For hyperdiverse groups with large numbers of rare species, more intensive sampling (i.e., larger numbers of subsamples) typically never generate curves that completely flatten out and reach an asymptote. For these taxa, rates of species accumulation are expected to slowly decrease with more sampling. The entire area may need to be exhaustively surveyed before one can be sure that every species has been collected, but in most cases complete sampling is not possible and is often not the objective.

Sufficient sampling for a high level of completeness is therefore the point at which the accumulation curves show an adequate decrease in species detection. The problem is the lack of existence of an asymptote for diverse taxa and the difficulty in quantifying “an adequate decrease in

species detection.” One possibility is to sample until a certain percentage—say, 80%—of the estimated species are sampled. In this study, between 78% and 82% of the species had been sampled from 50 stations based on ICE and jackknife estimates of species richness (Table 9-4). For all elevations combined, 86% of the ICE and 82% of the jackknife-estimated species richnesses were sampled. The problem with this approach is that the ICE and jackknife-estimated values are sensitive to sample size (Fig. 9-2). For example, after 10 stations, comparable percentages of ICE and jackknife estimates were obtained, but species accumulation was still rising rapidly. Therefore, the percentage sampled of the ICE and jackknife-estimated species richness was not a reliable indicator of completeness. For example, at 1250 m (Fig. 9-2a), the ICE, jackknife, and observed curves between 10 and 50 stations are parallel. ICE and jackknife estimates predict comparable levels of completeness within this range of samples (10–50) even though species accumulation was still rising rapidly after 10 stations (Fig. 9-2a). Sensitivity to sample size prevents using this method for assessing the level of completeness of these inventories.

An alternative approach is to sample until additional sampling efforts achieve a defined percentage increase in the number of species sampled. Species accumulation curves can be extrap-

TABLE 9-11. Complementarity (M-S, above the diagonal) and beta-1 (below the diagonal) diversity values for the 800 m zone sites between the RNI d'Andohahela, the RNI d'Andringitra, the RS d'Anjanaharibe-Sud, and the western Masoala Peninsula. Data from the 785 and 825 m transects from the RNI d'Andringitra were combined. The numbers (percentage) of species specific to the locality within the 800 m zone are presented along the diagonal. Total number of species for all 800 m sites is 242.

	Andohahela	Andringitra	Anjanaharibe-Sud	Masoala
Andohahela	25 (35)	0.664	0.880	0.861
Andringitra	0.487	37 (42)	0.886	0.848
Anjanaharibe-Sud	0.786	0.795	45 (46)	0.714
Masoala	0.756	0.763	0.563	50 (46)

TABLE 9-12. Complementarity (M-S, above the diagonal) and beta-1 (below the diagonal) diversity values for the 1200 m zone sites between the RNI d'Andohahela, the RNI d'Andringitra, and the RS d'Anjanaharibe-Sud. The numbers (percentage) of species specific to the locality within the 1200 m zone are presented along the diagonal. Total number of species for all 1200 m sites is 151.

	Ando- hahela	Andrin- gitra	Anjana- haribe-Sud
Andohahela	32 (54)	0.795	0.867
Andringitra	0.660	23 (56)	0.933
Anjanaharibe-Sud	0.766	0.874	68 (79)

olated to project the increase in species richness expected for a increase in sampling effort (Soberón & Llorente, 1993; Colwell & Coddington, 1994). In Figure 9-3, I fitted the observed species accumulation curves using the Soberón and Llorente (1993) logarithmic model: $S(t) = \ln(1 + zat)/z$, where t is the measure of sampling effort (samples or individuals), and z and a are curve-fitting parameters. Log models do not have an asymptote and are considered appropriate for species-rich taxa (Soberón & Llorente, 1993). That is, I use a nonasymptotic model because I assume the curves will never completely flatten, even with complete sampling. Using a nonasymptotic model may therefore result in a conservative estimate of the number of species predicted with increasing effort. I fitted the log model using the nonlinear least squares method of regression in JMP (SAS Institute, 1994). Based on the extrapolation of these curves, a doubling of sampling effort (an additional 50 stations) would achieve only a 13% gain in species richness at the 430 m site, 14% at 800 m, and 15% at 1250 m (Fig. 9-3). If all samples are combined, only 17 more species (13%) are predicted from a doubling of sampling effort (an additional 150 stations).

The relative between-site pattern of species richness would change very little if collection had been made at an additional 50 stations at each elevation. The relative ranking of between-site pattern of species richness stabilized after a few stations (Table 9-5) and is not predicted to change with the addition of 50 more stations at each transect.

Additional species from 100 station transects, however, could affect the relative between-site pattern of complementarity. If increased sampling collects rare species that are restricted to a particular elevation, then complementarity can be un-

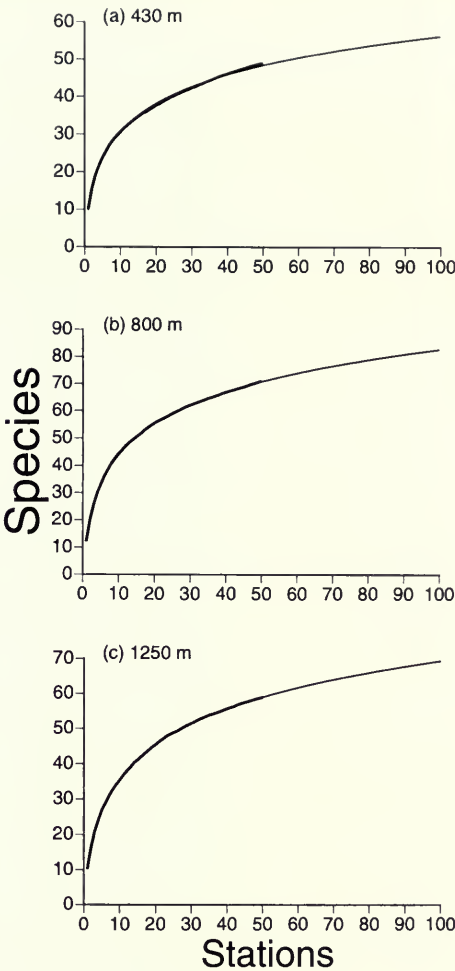


FIG. 9-3. Projection of species accumulation curves for each elevation (a–c) in the RNI d'Andohahela. The *thick line* corresponds to the observed species for the 50 stations sampled. The *thin line* is the logarithmic function fitted to the observed species curve by standard least squares method. The logarithmic curves predict the number of species expected from a doubling of sampling effort (100 stations).

derestimated with the 50-station transect. Complementarity is initially overestimated, on the other hand, if additional sampling collects rare species that are also widespread and found at one or more other sites, or collects rare species at a site that are commonly found at one or more other sites. The problem is that we do not know the identity of the unsampled species or the direction of the bias.

The stability of the complementarity values between sites at 50 samples can be evaluated by examining smoothed complementarity accumula-

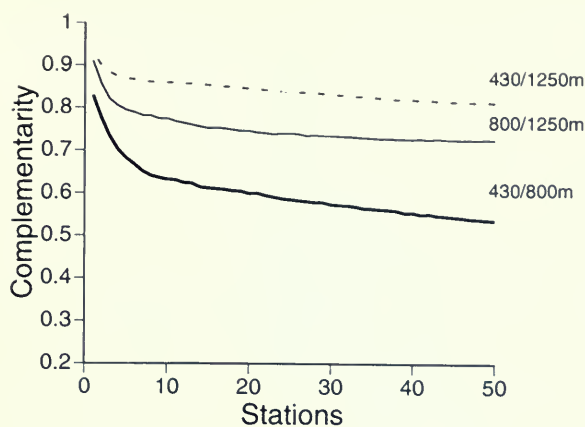


FIG. 9-4. Complementarity (M-S) accumulation curves for each between-site comparison in the RNI d'Andohahela. Each curve is plotted from the mean complementarity value of 100 randomizations of sample accumulation order.

tion curves, which were produced by calculating mean complementarity values for each value of n between 1 and 50 chosen from each site, with 100 random reorderings of sample order (J. A. Umbanhowar, unpubl. program). For example, for $n = 5$, five samples were chosen from each site and the complementarity value calculated. This was repeated 99 times, and each time sample order was randomized. These 100 complementarity values were used to compute the mean for $n = 5$.

For RNI d'Andohahela, the relative ranking of between-site complementarity values stabilized after a few stations were sampled (Fig. 9-4). The relative magnitude of between-site complementarity generally stabilized after about 25 samples. With increased sampling, however, the 430 and 800 m comparison showed an almost linear decrease in complementarity. The analysis of complementarity accumulation curves suggests that the rate of accumulation of rare and shared species is relatively constant and will change little with additional collecting.

For the goals of this study, a doubling of the number of stations sampled—and the subsequent increase in the time spent sorting, identifying, and curating the additional specimens—is not worth the minimal gain in information (estimated 13% gain in number of species). It appears that relative patterns of species richness and complementarity would change little with additional collecting. What is lost, however, is the identity of the additional species that could be collected. Different criteria would apply for evaluating inventories addressing questions about faunal composition

(identity), as opposed to species diversity and complementarity.

For all elevations sampled, therefore, species accumulation curves indicate that with increased sampling effort using the same methods (i.e., adding more pitfall and litter stations) in the same area, only marginal increases in species richness would be attained. The ICE and jackknife estimates of the actual species richnesses were almost identical for each elevation when all stations were pooled (Fig. 9-2) and were between 4% and 9% greater than the species richness predicted from 100 station samples. The precision of the ICE and jackknife estimators is difficult to determine because a site would need to be exhaustively surveyed to produce a complete species list. Nevertheless, these results show that the inventory techniques used in this study provide sufficient sampling for comparisons of species richness, faunal similarity, and species turnover among sites.

Comparisons with Other Faunas

The degree of complementarity (M-S index) at the local scale of between elevations (54–81%) was similar to the level of distinctness between localities (65–87%). The distance between localities and the elevations surveyed within each locality affect complementarity (compare the RNI d'Andohahela and the RNI d'Andringitra, with the RS d'Anjanaharibe-Sud and the western Masoala Peninsula; Table 9-10). For the 800 m zone comparison (Table 9-11) there was a positive re-

lationship between the distance separating localities and complementarity values measured as the M-S index ($r^2 = 0.83$).

The relative prevalence of species from the subfamily Ponerinae and Myrmicinae was similar for the 800 and 1250 m sites (0.41 and 0.42, respectively, Table 9-3). The Ponerinae/Myrmicinae (P/M) ratio for 430 m (0.19) was smaller because of a fewer number of ponerine species present. At the 425 m site on the western Masoala Peninsula, however, 24 species with a relative prevalence of 24% were found (Fisher, 1998, Table 4-6). The 1985 m site in the RS d'Anjanaharibe-Sud is the only elevation surveyed with a similar low P/M ratio (P/M = 0.17 with nine species total; Fisher, 1998). The region- and elevation-specific P/M ratios in Madagascar preclude the use of the P/M ratio to estimate whole ant faunas (Fisher, 1998).

Conclusion

An evaluation of the efficacy of the transect methods suggests that even though increased sampling would collect new species, the results for relative species richness and complementarity values between sites in the RNI d'Andohahela would change little. To better understand the effect of scale on these results, additional surveys are needed. Replicate transects at various distances apart at the same elevation in the RNI d'Andohahela would provide information on the scale of species turnover at a specific elevation in the reserve and would indicate which patterns of species richness and composition at one transect are characteristic of that elevation.

Inventories provide baseline information for understanding geographic variation in biotic assemblages. They are the first step to defining areas of endemism and patterns of species richness. In addition, these inventory methods provide a new tool for evaluating environmental change.

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Chapter 10

Taxonomic and Ecological Observations on the Scorpions Collected in the Réserve Naturelle Intégrale d'Andohahela, Madagascar

Wilson R. Lourenço¹ and Steven M. Goodman²

Abstract

An elevational transect of the scorpion fauna of parcel 1 and a general survey of parcel 2 in the Réserve Naturelle Intégrale d'Andohahela is reported. Six species of scorpions were collected in the reserve, including three in the humid forest of parcel 1 and three in the dry forests (spiny bush) of parcel 2. Although these two parcels are separated only by 20 km, their scorpion faunas contain no species in common. These collections yielded three species previously unknown to science, two of which have recently been described and the third of which is named here.

Résumé

Un "transect" altitudinal de la faune scorpionique de la parcelle 1, et un inventaire de celle de la parcelle 2 de la Réserve Naturelle Intégrale d'Andohahela sont rapportés dans ce travail. Six espèces de scorpions ont été collectées dans la réserve, trois d'entre elles dans la forêt humide de la parcelle 1 et trois dans les forêts sèches de la parcelle 2. Bien que ces deux parcelles soient séparées par seulement 20 km, leur faunes scorpioniques respectives ne présentent aucune espèce commune. Parmi les scorpions collectés, trois correspondaient à des espèces nouvelles, deux ont été décrites récemment et la troisième est décrite à présent.

Introduction

In recent years there has been increased interest in the scorpions of Madagascar (see Lourenço, 1996, for summary). Most of the scorpion material amassed on Madagascar to date has been the result of relatively random opportunistic collecting, however, and few sites have been surveyed systematically. The known scorpion faunas of in-

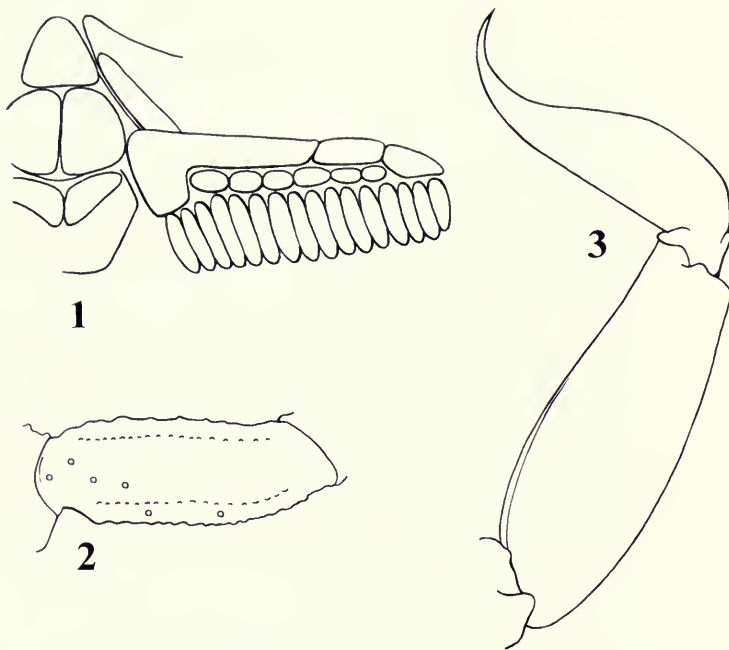
dividual sites are generally incomplete; this in turn hampers any detailed zoogeographical analysis of the island's fauna.

Methods

During the 1995 mission to the Réserve Naturelle Intégrale (RNI) d'Andohahela a collection of scorpions was made by S. M. Goodman, B. L. Fisher, and M. Pidgeon. Habitats sampled include the humid forests of parcel 1, within an elevational range of 400 to 1956 m, and the spiny bush of parcel 2, at 120 m (see Chapter 2). Although

¹Laboratoire de Zoologie (Arthropodes), Muséum National d'Histoire Naturelle, 61, rue de Buffon, 75005 Paris, France.

²Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, Illinois 60605-2496, U.S.A.



FIGS. 10-1 to 10-3. *Pseudouroplectes pidgeoni*, n. sp. Male holotype. (1) Sternum, genital operculum and pectine. (2) Femur, dorsal aspect, showing the A- α trichobothrial configuration. (3) Metasomal segment V and telson, lateral aspect.

we do not consider this collection to have been sufficiently exhaustive to reflect the complete scorpion fauna of the reserve, the use of systematic techniques at each site permits comparison of the results. Collection procedures in both parcels included pitfall buckets (see Chapter 12) and leaf litter sampling (Chapter 9). Furthermore, in parcel 2 active searching under fallen wood and rocks was also employed.

The first batch of material from the RNI d'Andohahela was sent to W. R. Lourenço while he was preparing a monograph on the scorpion fauna of Madagascar. On the basis of this material two species new to science were described (Lourenço, 1996). Since the publication of this work other specimens from the site have been studied. These include a representative of a third species new to science that is described here. Information is also provided on other records of scorpions from in and around the RNI d'Andohahela.

Results

Scorpions were collected from three of the six sites sampled in the RNI d'Andohahela: in humid

forest in parcel 1, at 440 and 810 m, and in spiny bush in parcel 2, at 120 m. A total of six species were recorded, one of which is described below.

Pseudouroplectes pidgeoni Lourenço & Goodman, new species (Figs. 10-1 to 10-3)

HOLOTYPE (MALE)—Madagascar, Province de Toliara, Réserve Naturelle Intégrale d'Andohahela, parcel 2, 7.5 km E-NE of Hazofotsy, 46°36.6'E, 24°49'S, 120 m, between 7 and 15 December 1995, collected by M. Pidgeon. The specimen was in a soil litter sample at the edge of pitfall line 18. Deposited in the Field Museum of Natural History, Chicago.

ETYMOLOGY—It is with pleasure that we name this species after Mark Pidgeon, who collected the holotype during the 1995 expedition to the reserve. His participation in the mission and many years of field experience on Madagascar are gratefully acknowledged.

DIAGNOSIS—Very small scorpion, with a total length between 13 and 14 mm. The body is very slender and flattened. General coloration yellowish; presence of four longitudinal reddish brown stripes extending from the posterior margin of carapace to the keels of tergite VII. It may be

TABLE 10-1. Morphometric values of the male holotype of *Pseudouroplectes pidgeoni*.

Character	Measurement (mm)
Carapace	
length	1.7
anterior width	1.1
posterior width	1.6
Metasomal segment I	
length	0.9
width	1.0
Metasomal segment V	
length	2.1
width	1.0
depth	0.9
Vesicle	
width	0.5
depth	0.5
Pedipalp	
Femur length	1.2
Tibia length	1.7
Chelae length	2.2
Movable finger	
length	1.6

distinguished from *Pseudouroplectes betschi*, the first species described in this genus, by the presence of these four stripes, which are absent on *P. betschi*. The description is based on the male holotype, and measurements are presented in Table 10-1.

COLORATION—Prosoma and mesosomal dorsum yellowish, with four longitudinal reddish brown stripes that commence at the posterior margins of the carapace and extend over the tergites to the keels of tergite VII. Eyes surrounded with black pigment. Metasoma: all segments yellowish, with reddish brown pigment underlining the keels. Vesicle yellowish, without spots. Venter yellowish. Chelicerae yellowish without spots; fingers pale reddish. Pedipalps yellowish, with some vestigial reddish zones; fingers pale yellow, with reddish granulation. Legs yellowish.

MORPHOLOGY—Carapace with feeble but regular granulation; anterior margin with a very slight median concavity. Anterior median superciliary and posterior median keels very weak, only vestigial. All furrows not particularly pronounced. Median ocular tubercle distinctly anterior to the center; median eyes separated by slightly less than one ocular diameter. Three pairs of lateral eyes. Sternum subpentagonal to pentagonal. Tergites

mesosoma feebly granular. Median keel moderate to feeble on all tergites. Tergite VII pentacarinat. Venter: genital operculum divided longitudinally. Pectines: pectinal tooth count 16–17; basal middle lamellae of the pectines not dilated; fulcra absent. Sternites smooth with short linear stigmata; VII without keels. Metasoma: segments I and II of metasoma with eight crenulate keels; segment III with six crenulate keels; segment IV with four crenulate keels; segment V with two vestigial keels. Ventral keels absent on all segments. Dorsal keels on segments I to IV with some posterior spinoid granules. Intercarinal spaces smooth. Telson smooth with a short and moderately curved aculeus and numerous setae. Cheliceral dentition characteristic of the family Buthidae (Vachon, 1963); ventral aspect of both finger and manus with dense fine setae. Pedipalps: femur pentacarinat; tibia and chelae with some moderately crenulate keels; internal face of tibia with some spinoid granules; all faces moderate to feebly granular. Movable finger of chela with seven linear rows of granules; accessory granules absent. Trichobothriotaxy, A- α (Vachon, 1973, 1975). Legs: tarsus with very numerous fine setae ventrally. Tibial spurs absent.

Known Scorpion Fauna of the RNI d'Andohahela

HUMID FOREST (PARCEL 1)—At 400 m in low-land humid forest the collections included nine specimens (all males) of *Heteroscorpion goodmani* Lourenço, 1996, family Heteroscorpionidae, and eight specimens (six males and two females) of *Grosphus madagascariensis* (Gervais, 1844), family Buthidae. These specimens were taken in a single pitfall line. A second pitfall line installed at 440 m yielded nine specimens (seven males and two females) of *Heteroscorpion goodmani* and five specimens (all male) of *Grosphus madagascariensis*. During the night numerous individuals of *H. goodmani* were observed with a standard flashlight on trunks of canopy trees within 2–3 m of the ground. Within the same elevational zone a single female specimen of *Tityobuthus parrilloi* Lourenço, 1996, family Buthidae, was collected in a leaf litter sample. At 810 m three specimens (two males and one female) of *Grosphus madagascariensis* were collected in the three pitfall lines. No scorpions were collected when these same devices were used within the 1200, 1500, and 1875 m zones. Furthermore, no scorpion was

obtained in the leaf litter samples from these three elevational zones.

SPINY BUSH (PARCEL 2)—Scorpions were relatively common in the spiny bush habitat of this parcel. The site surveyed was at 120 m, and all specimens were obtained within ± 20 m. The individual collections included: (1) two specimens, one adult male and one immature male, of *Grosphus grandidieri* Kraepelin, 1901; (2) one male of *Grosphus grandidieri*, along with 14 specimens (10 males and four females) of *Opisthacanthus punctulatus* Pocock, 1896; (3) 13 specimens (seven males and six females) of *Opisthacanthus punctulatus*, which were collected under rocks and dead wood during the day; (4) 14 individuals (12 males and two females) of *Opisthacanthus punctulatus*, from under rocks; (5) eight specimens (three males and five females—juveniles), of *Opisthacanthus punctulatus*, from forest litter; and (6) one male specimen of *Pseudouroplectes pigeoni* nov. sp., family Buthidae, in a litter sample.

Other Records from the Area

Several other records of the scorpion fauna of the region have been reported (Lourenço, 1996). These records include material obtained during the 1995 expedition to the RNI d'Andohahela and earlier collections from the reserve and neighboring areas. *Grosphus madagascariensis* was obtained 30–35 km NW of Fort Dauphin (Tolagnaro), Forêt d'Isaka (probably Isaka-Ivondro), in December 1901 by C. Alluaud. Furthermore, an immature male of this species and one female of *Tityobuthus parrilloi* Lourenço, 1996, were collected at 430 m along the northern boundary trail of parcel 1 on 24 November 1992 by B. L. Fisher. Finally, in this same region of the reserve but on slightly higher ground at 650 m, an immature male of *G. madagascariensis* was collected on 19 November 1992 by B. L. Fisher. *Opisthacanthus punctulatus* has been reported from parcel 2 at 46°36'E, 24°49'S (Lourenço, 1996).

Discussion

Among the specimens collected using pitfall buckets, males are dramatically more numerous than females. This is easy to explain, however, because male scorpions are much more active

TABLE 10-2. The known scorpion fauna of parcels 1 and 2 of the RNI d'Andohahela.

Species	Parcel 1	Parcel 2
BUTHIDAE		
<i>Grosphus grandidieri</i>		120 m
<i>Grosphus madagascariensis</i>	400–810 m	
<i>Pseudouroplectes pigeoni</i>		120 m
<i>Tityobuthus parrilloi</i>	430–440 m	
HETEROSCORPIONIDAE		
<i>Heteroscorpion goodmani</i>	400–440 m	
ISCHNURIDAE		
<i>Opisthacanthus punctulatus</i>		120 m
Total number of species	3	3

than females, particularly during the reproductive season. In general, scorpions reproduce during the rainy season (Lourenço, 1991, 1995). In the case of the RNI d'Andohahela, most of the scorpions were collected in the 440 m zone between 21 and 28 October 1995. During this 7 day period, 37.7 mm of rain was recorded. In southeastern Madagascar the actual start of the rainy season is variable between years and gradually commences during the month of October (Donque, 1975; Ratsivalaka-Randriamanga, 1985).

Four of the six males of *Grosphus madagascariensis* collected in the 400 m elevational zone had spermatophores in a final phase of ejection and ready for deposition over the substrate. This suggests that these males, in the presence of females, may have commenced some aspects of breeding courtship after they had fallen into the pitfall buckets.

On the basis of the collected material, the altitudinal and habitat characteristics of each species are relatively limited (Table 10-2). This is in accordance with the general pattern of scorpions having strict ecological requirements, with many classified as equilibrium species (Lourenço, 1991). The exception to this case is *Grosphus madagascariensis*, which was found in a broader range of elevations in lowland humid forest between 400 and 810 m, although within this altitudinal range the habitat is rather homogeneous. This species has a broad geographical range, including Nosy Be in the northwest, and it occurs throughout much of the eastern humid forests from the RNI d'Marojejy south to Tolagnaro (Lourenço, 1996).

The vegetation of parcel 1 is distinctly different from that of parcel 2, with the former being char-

acterized by its humid forest and the latter by its xerophytic bush. Between the two parcels, which are separated by an air distance of about 20 km, there is a remarkable change in the climate and flora across the rain shadow of the Anosyenne Mountains. Rain systems moving in from the eastern coast of Madagascar release their precipitation along the eastern slopes of the Anosyenne Mountains (Donque, 1972). This ecotone between wet and dry is known to be a major barrier to dispersal for certain groups of land vertebrates (see, e.g., Goodman et al., 1997). In the scorpion fauna no species is shared in common between the two parcels and faunal turnover is complete.

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Chapter 11

Amphibians and Reptiles of the Réserve Naturelle Intégrale d'Andohahela, Madagascar

Ronald A. Nussbaum,¹ Christopher J. Raxworthy,² Achille P. Raselimanana,³ and Jean-Baptiste Ramanamanjato⁴

Abstract

The Réserve Naturelle Intégrale (RNI) d'Andohahela, consisting of three parcels, is located in southeastern Madagascar near the city of Tolagnaro. Parcel 1 is a large (63,100 ha) rain forest reserve with a wide elevational range (90–1972 m) that lies on the eastern flank of the Anosyenne Mountains. The smaller (12,420 ha) parcel 2 occurs in the rain shadow of the Anosyenne Mountains about 5 km west of parcel 1 at their closest points. Parcel 2 is generally lower in elevation (120–1006 m) than parcel 1, much drier, and supports only spiny forest and some gallery forest.

We surveyed the herpetofaunas of parcels 1 and 2 at the beginning of the warm rainy season between 18 October and 14 December 1995. Five sites along an elevational transect (440, 810, 1200, 1500, and 1875 m) were visited for periods of 8–10 days in parcel 1, and a single site was visited for 7 days in parcel 2. Species accumulation curves indicate that the five sites in parcel 1 were adequately surveyed, but the curve for the single site in parcel 2 suggests that additional species might have been found with a longer survey period.

Pitfall trapping (1,485 trap-days) yielded 45 captures of 13 species of amphibians and reptiles, for an overall daily trap success of 3.0%. This trap success is similar to results for many other sites in Madagascar.

Forty-five amphibian and 32 reptile species were found in parcel 1. Amphibians were more diverse than reptiles at all sites (elevations) with the exception of the highest site (1875 m), where reptiles were more diverse. As has been reported for other rain forests in Madagascar, herpetofaunal diversity increases slightly from the lower elevations to the mid-altitude forests and then declines sharply at the higher elevations. These altitudinal changes in diversity are accompanied by an altitudinal turnover of species, with the maximum turnover at about 1200 m in parcel 1. The discovery of several species in parcel 1, for example the colubrid snake *Pseudoxyrhopus tritaeniatus* and the gekkonid *Lygodactylus montanus*, extends their geographical ranges considerably to the south in Madagascar. A new day gecko (*Phelsuma*) is the only species endemic to parcel 1. In general, the herpetofauna of parcel 1 is representative of the broader herpetofauna of the nearby Anosyenne and Vohimena mountains.

The herpetofaunal diversity of parcel 1, with 77 species of amphibians and reptiles, is similar

¹ Division of Amphibians and Reptiles, Museum of Zoology, University of Michigan, Ann Arbor, MI 48109-1079, U.S.A.

² CERC, Department of Biology, Columbia University, New York, New York 10277, U.S.A. *Current address:* Division of Herpetology, Natural History Museum, Department of Systematics and Ecology, University of Kansas, Lawrence, KS 66045, U.S.A.

³ World Wide Fund for Nature, Madagascar, B.P. 738, Antananarivo (101), Madagascar.

⁴ Département de Biologie Animale, Université d'Antananarivo, B.P. 906, Antananarivo (101), Madagascar.

to that of other rain forest reserves located further to the north in Madagascar. Parcel 1 is more diverse than the Parc National de la Montagne d'Ambre (70 species) but less diverse than the Réserve Spéciale d'Anjanaharibe-Sud (93 species) and the Réserve Naturelle Intégrale/d'Andringitra (92 species). As expected, the herpetofauna of parcel 1 is more similar to that of Andringitra, lying 285 km to the north, than it is to either Anjanaharibe-Sud (1,070 km north) or Montagne d'Ambre (1,300 km north).

The dry spiny forests of parcel 2 yielded far fewer herpetofaunal species (34) than the rain forests of parcel 1 and, as is expected of drier habitats, the relative abundance of amphibian and reptile species is reversed. Only four amphibian species were recorded in parcel 2, compared to 30 reptile species. In spite of the close proximity (5 km), there is almost total dissimilarity between the herpetofaunas of parcels 1 and 2, with only one shared species, a semi-burrowing skink, *Amphiglossus ornaticeps*. The herpetofauna of parcel 2 contains no locally endemic species and is generally representative of the southwestern dry spiny forests.

Although the Andohahela reserve contains only a single endemic herpetofaunal species (*Phelsuma*), it is critically important in protecting several species that have limited distributions and whose survival may ultimately depend on protection within the reserve system. Uncommon southern species that were previously unknown in parcel 1, but were recorded there during this survey, are the mantellid frog, *Mantella haraldmeieri*, the chameleon, *Calumma capuroni*, and the two geckos *Uroplatus malama* and *U. malahelo*. Another rare regional endemic, the day gecko *P. antanosy*, was not found in parcel 1.

Résumé

La RNI d'Andohahela composée de trois parcelles est située dans le Sud-Est de Madagascar. La parcelle 1 est une vaste Réserve de forêt tropicale humide (63.100 ha) avec une grande variété d'altitudes (90 m–1972 m) étalée sur le versant Est des montagnes Anosyennes.

La plus petite parcelle, la parcelle 2 (12.420 ha) se trouve sous l'influence permanente de la pluie des montagnes Anosyennes, à environ 5 km à l'Ouest de la limite de la parcelle 1. La parcelle 2 possède moins de variété d'altitudes (120 m–1006 m) que la parcelle 1 et plus sèche, abritant seulement de la forêt broussailleuse et épineuse et quelque forêt galerie.

La Parcelle 3 (500 ha), également un site sec de basse altitude, s'étale au Sud de la parcelle 2 et comprend de la forêt épineuse dégradée, sèche et à feuilles caduques.

Les herpetofaunes des parcelles 1 et 2 ont été inventoriées au début de la saison chaude et pluvieuse entre le 20 octobre et le 13 décembre 1995. Cinq sites se trouvant le long d'un transect altitudinal (à 440 m, 810 m, 1200 m, 1500 m, et 1875 m) ont été visités pendant une période de 8 à 10 jours pour la parcelle 1, et un seul site a été visité pendant 7 jours pour la parcelle 2. Les courbes sur la concentration des espèces démontrent que les cinq sites de la parcelle 1 ont été inventoriés convenablement, mais la courbe pour le seul site de la parcelle 2 suppose que d'autres espèces pourraient être découvertes au bout d'une étude plus prolongée.

Les pièges à trous installées pendant 1.485 jours trou-pièges ont résulté en 35 captures de 13 espèces d'amphibiens et reptiles, avec un taux global de réussite journalier de 3%. Ce taux de capture est similaire aux résultats acquis dans les autres sites de Madagascar.

Quarante-cinq espèces d'amphibiens et 32 reptiles ont été découvertes dans la parcelle 1. Les amphibiens sont plus diversifiés par rapport aux reptiles dans tous les sites de différentes altitudes à l'exception du plus haut site (1875 m), où les reptiles sont plus diversifiés. Selon les rapports sur les différentes forêts tropicales humides de Madagascar, la diversité en herpetofaune augmente légèrement des forêts de basse altitude vers une altitude moyenne et puis diminue considérablement en haute altitude.

Ces changements altitudinaux en diversité sont accompagnés par une apparition des espèces selon l'altitude, avec un maximum d'apparition à environ 1200 m dans la parcelle 1. La découverte de plusieurs espèces dans la parcelle 1 par exemple le serpent colubrid *Pseudoxyrhopus tritaeniatius* et le geckonid *Lygodactylus montanus*, élargit considérablement l'aire géographique de répartition vers le Sud de Madagascar. Il y a uniquement une espèce endémique

dans la parcelle 1, qui est une nouvelle espèce diurne de gecko (*Phelsuma*). En général, l'herpetofaune de la parcelle 1 est représentative de l'ensemble d'herpetofaune des montagnes avoisinantes d'Anosy et de Vohimena.

La diversité en herpetofaune de la parcelle 1, avec 77 espèces d'amphibiens et de reptiles, est similaire à celle des autres Réserves de forêt tropicale humide situées dans le Nord de Madagascar. La parcelle 1 d'Andohahela est plus diversifiée que le Parc National de la Montagne d'Ambre (70 espèces), mais moins diversifiée que la Réserve Spéciale d'Anjanaharibe-Sud (93 espèces) et la Réserve Naturelle Intégrale d'Andringitra (92 espèces). Selon les attentes, l'herpetofaune de la parcelle 1 est plus similaire à celle d'Andringitra, s'étalant sur 285 km vers le Nord, par rapport à Anjanaharibe-Sud (1.070 km au Nord) ou Montagne d'Ambre (1.300 km au Nord).

Les forêts sèches et épineuses de la parcelle 2 renferment moins d'espèces en herpetofaune (34) que les forêts humides de la parcelle 1, et selon les attentes pour les habitats plus secs, l'abondance relative des espèces d'amphibiens et de reptiles est renversée. Seulement 4 espèces d'amphibiens sont inventoriées dans la parcelle 2 comparées à 30 espèces de reptiles. Malgré la proximité exiguë (5 km), il y a presque une dissimilarité totale entre les herpetofaunes des Parcelles 1 et 2, avec seulement une espèce commune, un lézard fouisseur, *Amphiglossus ornateps*. L'herpetofaune de la parcelle 2 ne contient aucune espèce endémique et est généralement représentative des forêts sèches et épineuses du Sud-Ouest de Madagascar.

Bien que la RNI d'Andohahela contienne une seule espèce endémique (*Phelsuma*), il est extrêmement important de protéger plusieurs espèces dont la répartition est limitée et dont la survie pourrait en définitive dépendre de la protection de l'écosystème de la Réserve. Les espèces du Sud d'intérêt commercial qui auparavant ont été inconnues dans la parcelle 1 mais ont été inventoriées au cours de cette recherche, sont la grenouille mantellid, *Mantella haraldmeieri*, le caméléon, *Calumma capuroni*, et les deux geckos *Uroplatus malama* et *U. malahelo*. Une autre espèce rare, endémique de la région, le gecko diurne *P. antanosy*, n'a pas été découverte dans la parcelle 1.

Introduction

Since 1989 considerable new information on the diversity and distribution of amphibians and reptiles in Madagascar has accumulated as a result of surveys done by field teams from the Museum of Zoology, the University of Michigan; Département de Biologie Animale, Université d'Antananarivo; Museum Alexander Koenig, Bonn; and Museo Regionale di Scienze Naturali, Torino. Our ongoing "Michigan" program included intensive herpetofaunal surveys of 28 reserves and numerous other sites throughout the wet, dry, and transitional forests of Madagascar.

The results of our studies to date include the description of 26 new species of reptiles (Nussbaum & Raxworthy, 1994a–d, 1995a–c, 1998a,b; Nussbaum et al., 1998a,b; Raxworthy & Nussbaum, 1993a,b, 1994a,b, 1995) and one new small mammal of the family Tenrecidae (Jenkins et al., 1997). Approximately 100 new species of amphibians and reptiles resulting from the Michigan surveys in Madagascar remain to be described. In addition to taxonomic studies, we have analyzed

distributional patterns in a series of papers addressing (1) the herpetofauna of specific reserves (Raxworthy & Nussbaum, 1994c, 1996a; Raxworthy et al., 1998); (2) montane communities of amphibians and reptiles (Raxworthy & Nussbaum, 1996b); (3) patterns of endemism of terrestrial vertebrates in eastern Madagascar (Raxworthy & Nussbaum, 1996c); and (4) biogeographical patterns of reptiles in relation to named phytogeographic zones in eastern Madagascar (Raxworthy & Nussbaum, 1997).

We described in detail the herpetofaunal diversity of three rain forest sites, beginning with the extreme northern Parc National (PN) de la Montagne d'Ambre (Raxworthy & Nussbaum, 1994c), the north-central Réserve Spéciale (RS) d'Anjanaharibe-Sud (Raxworthy et al., 1998), and the south-central Réserve Naturelle Intégrale (RNI) d'Andringitra (Raxworthy & Nussbaum, 1996a). We have now surveyed the southernmost reserve in Madagascar, RNI d'Andohahela, which includes both rain forest and dry spiny forest. The main objective of this report is to describe the herpetofauna of the RNI d'Andohahela and place

it in biogeographical perspective with other nearby and distant sites.

The three parcels of RNI d'Andohahela lie in the southern Anosyenne Mountains about 35 km west-northwest of Tolagnaro. Aspects of the physical environment of Andohahela and the surrounding area were described by Paulian et al. (1973), Nicoll and Langrand (1989), and Goodman et al. (1997). Climates are seasonal in this region, with the cool, dry (winter) period occurring from May through October and the wet, warm (summer) period from November through April. The average annual temperature near Tolagnaro is 23°C, with monthly averages ranging from a low of 16°C in July to a high of 29°C in January. Precipitation is highly variable in this region, depending on both season and local topography.

Parcel 1, the largest (63,100 ha) of the three parcels, lies on the eastern flank of the Anosyenne Mountains and is blanketed with rain forest. Elevations in parcel 1 range from about 90 to 1,972 m, and the vegetation changes with altitude, from high canopy, lowland rain forest to low canopy, high montane, sclerophyllous forest. Rainfall is high, ranging from about 1,500 to 3,000 mm per annum for six stations east of the crest of the Anosyenne Mountains, most of it coming during the 180 days of summer, November through April. Parcel 2 (12,420 ha) lies west of the Anosyenne Mountains at elevations from 120 to 1006 m. The vegetation of parcel 2 is largely spiny forest, with some gallery forest along the Mananara River. Precipitation in parcel 2 is much lower than in parcel 1, averaging only 600–700 mm per annum, with almost all of it occurring in the period November through April.

During late 1989 and 1990 we participated in a survey of littoral forests and other degraded lowland sites in the region of Tolagnaro with regard to the planned mining of titanium oxide (ilmenite) sands by QIT FER Madagascar Minerals, Inc. In addition to surveying within the proposed mining zone, we also surveyed several surrounding sites outside the mining zone in order to better understand the potential impact of the proposed exploitation on the southeastern herpetofauna. Since 1990 we have surveyed with various degrees of intensity many other sites in southern Madagascar, and we will draw on this unpublished information for comparative purposes.

Literature on the herpetofauna of the RNI d'Andohahela is sparse. A French expedition during 1971–1972 to the Anosyenne Mountains (Paulian et al., 1973) resulted in collections of am-

phibians and reptiles, but apparently the results have not been published. Nicoll and Langrand (1989) summarized the vertebrate faunas of most Malagasy reserves, but their list for Andohahela includes no amphibians and reptiles. One thesis and two memoirs have been written concerning the herpetofauna of the Tolagnaro region (Ramanamanjato, 1993; Raselimanana, 1993; Morris, 1994), but these do not include data from the RNI d'Andohahela. Andreone and Randriamahazo (1997) presented herpetofaunal data for low-altitude rain forest within the boundaries of parcel 1 of the RNI d'Andohahela. The latter authors included literature records in their list of amphibians and reptiles for Andohahela. However, their literature records are apparently based on unverified reports and include records of species from localities near to, but not actually within, the reserve.

Study Sites

The five survey sites in parcel 1 and the single survey site in parcel 2 of RNI d'Andohahela are listed below. They were centered around the specified localities.

Site 1 (440 m)—8 km NW of Eminiminy; 46°45.92'E, 24°37.55'S; surveyed 18–28 October 1995.

Site 2 (810 m)—12.5 km NW of Eminiminy; 46°44.30'E, 24°35.60'S; surveyed 28 October–6 November 1995.

Site 3 (1200 m)—13.5 km NW of Eminiminy; 46°44.08'E, 24°35.04'S; surveyed 7–16 November 1995.

Site 4 (1500 m)—15 km NW of Eminiminy; 46°43.85'E, 24°34.15'S; surveyed 17–26 November 1995.

Site 5 (1875 m)—20 km SE of Andranondambo; 46°43.30'E, 24°30.70'S; surveyed 27 November–3 December 1995.

Site 6 (120 m)—The single site surveyed in parcel 2 was located 7.5 km ENE of Hazofotsy; 46°36.60'E, 24°49.00'S; surveyed 7–14 December 1995.

Methods

The 1995 survey of parcel 1 began in October near the start of the rainy season and ended in December. Because the heaviest rainfall and

warmest temperatures usually occur in January, the survey period was suboptimal in regard to maximum amphibian and reptile activity. The two members of the herpetofaunal survey team were A.P.R. and J.B.R. Field techniques used to sample animals were (1) pitfall trapping with drift fences, (2) opportunistic day and night searching, and (3) refuge examination (under and in fallen logs and rotten tree stumps; under bark; under rocks; in leaf litter, root-mats, and soil; and in leaf axils of *Pandanus* screw palms and *Ravenala* traveller's palm).

Pitfall traps were buckets (275 mm deep, 290 mm top internal diameter, 220 mm bottom internal diameter) with the handles removed and small holes (2 mm diameter) punched in the bottom to allow water drainage. Buckets were sunk into the ground along a drift fence made from plastic sheeting (0.5 m) stapled to thin wooden stakes. The fence bottom was buried 50 mm deep into the ground using leaf litter. The drift fence (100 m in length) was positioned to run across the middle of each bucket. A bucket was placed at both ends of the drift fence, with nine additional buckets positioned along the drift fence at 10 m intervals. The trap lines were checked each morning and late afternoon, and captured animals were removed. After heavy rain the traps were sponged dry.

Three lines were used at each survey site. In parcel 1, lines were placed in the following forest types: ridge (along the crest of a ridge), slope (on a gradient, intermediate between ridgetop and valley bottom), and valley (within 20 m of a stream in a valley bottom).

Amphibians and reptiles were found by chance encounter and by searching for them in likely places during their active and basking periods. They were also sought in refuges. These searches were made throughout the full elevational range of habitats available in the reserve. The majority of searching was done close to trails made during the study, although ridges and riverbanks were also used to orient search paths. Night searching was done with the aid of headlamps.

The following information was recorded for each individual at the time of capture; date, time, altitude, microhabitat, and circumstances of capture. Representative individuals were photographed to preserve color. Animals not retained for specimens were returned to the site of original capture. Voucher specimens were fixed in 10% buffered formalin and later transferred to alcohol. Collected material was deposited in two research

collections: Département de Biologie Animale, Université d'Antananarivo (UABDA), and the Museum of Zoology, University of Michigan (UMMZ).

Results

A summary of the species found in both parcels 1 and 2 of Andohahela is given in Table 11-1. In the rain forests of parcel 1 (sites 1-5), 45 species of amphibians and 32 species of reptiles were discovered. In the dry spiny forests of parcel 2 (site 6), only four species of amphibians were found, but 30 species of reptiles were recorded. There was nearly complete dissimilarity between the herpetofaunas of parcels 1 and 2, with only one species, *Amphiglossus ornateiceps* (Reptilia, Scincidae), found in both parcels. The total herpetofaunal diversity of both parcels recorded by us is 110 species, including 49 species of amphibians and 61 species of reptiles.

Species accumulation curves (Fig. 11-1) provide information on the likely completeness of the survey. Although a few species were surely missed at each site, with the exception of site 6 our surveys were reasonably complete for the time of year that they were made.

A total of 1,485 pitfall trap-days yielded 45 captures of 13 herpetofaunal species (Tables 11-2 and 11-3; see also Chapter 13). Overall, herpetofaunal daily trap success was 3.0%, similar to that reported by Raxworthy and Nussbaum (1996a) and Raxworthy et al. (1998) for the RNI d'Andringitra (3.5%) and the RS d'Anjanaharibe-Sud (2.1%), respectively. The most productive pitfall lines were those at the lower elevations (lines 1-3), with daily trap capture success of 9-12%. The least productive lines were at the fourth (1500 m) and fifth (1875 m) sites, where just one capture was made in 495 bucket-days.

Within parcel 1 amphibian diversity exceeded that of reptiles (Table 11-1; Fig. 11-2) at all sites except at site 5, which is the highest elevation site. The mid-altitude "bulge" in herpetofaunal diversity for Madagascar that was reported and discussed elsewhere (Raxworthy et al., 1998) and the frequently observed trend for herpetofaunal diversity to decline at higher elevations (Raxworthy & Nussbaum, 1996a) are both evident for parcel 1 (Table 11-1; Fig. 11-2). As expected, because of the much drier aspect of parcel 2, reptiles were far more diverse than amphibians.

TABLE 11-1. Distribution of amphibians and reptiles in parcels 1 (sites 1–5) and parcel 2 (site 6) of the RNI d’Andohahela.

Species	Humid forest					Spiny forest	Elevation range (m)
	Site 1 440 m	Site 2 810 m	Site 3 1200 m	Site 4 1500 m	Site 5 1875 m	Site 6 120 m	
AMPHIBIA							
MANTELLIDAE							
<i>Laurentomantis ventrimaculatus</i>	x						500
<i>Mantella haraldmeieri</i>	x	x					400–780
<i>Mantidactylus aglavei</i>		x					810–820
<i>Mantidactylus albolineatus</i>			x	x	x		980–1900
<i>Mantidactylus bertini</i>				x			1400–1440
<i>Mantidactylus betsileanus</i>	x	x					430–800
<i>Mantidactylus bicalcaratus</i>		x					820–840
<i>Mantidactylus biporus</i>	x	x	x				430–1000
<i>Mantidactylus boulengeri</i>	x	x	x				420–1250
<i>Mantidactylus decaryi</i>		x	x	x			750–1450
<i>Mantidactylus depressiceps</i>		x		x			810–1500
<i>Mantidactylus eiselti</i>	x	x	x	x			430–1450
<i>Mantidactylus elegans</i>				x			1440
<i>Mantidactylus femoralis</i>	x	x	x	x			420–1450
<i>Mantidactylus guibei</i>				x	x		1450–1900
<i>Mantidactylus lugubris</i>	x	x	x				400–1100
<i>Mantidactylus luteus</i>		x	x				810–1200
<i>Mantidactylus microtis</i>			x	x			1100–1450
<i>Mantidactylus microtypanum</i>	x	x	x				400–1120
<i>Mantidactylus opiparis</i>	x	x	x				300–1050
<i>Mantidactylus spinifer</i>	x	x	x				420–1250
<i>Mantidactylus tornieri</i>	x	x					420–830
<i>Mantidactylus ulcerosus</i>	x						430–470
MICROHYLIDAE							
<i>Anodonthyla boulengeri</i>			x	x	x		440–1300
<i>Anodonthyla nigrigularis</i>	x	x	x				440–1200
<i>Madecassophryne truebae</i>		x					780
<i>Platypelis grandis</i>	x	x	x				420–1200
<i>Plethodonthyla bipunctata</i>	x	x	x				440–1110
<i>Plethodonthyla inguinalis</i>		x	x				820–1250
<i>Plethodonthyla laevipes</i>			x	x			1250–1590
<i>Plethodonthyla</i> sp. 1				x	x		1470–1900
<i>Plethodonthyla</i> sp. 2			x				1120
<i>Scaphiophryne brevis</i>						x	120
<i>Scaphiophryne calcarata</i>						x	120
RANIDAE							
<i>Ptychadena mascareniensis</i>						x	120
<i>Tomopterna labrosa</i>						x	120
RHACOPHORIDAE							
<i>Aglyptodactylus madagascariensis</i>	x						440
<i>Boophis albilabris</i>		x					810–820
<i>Boophis albipunctatus</i>	x	x	x				400–1130
<i>Boophis andohahela</i>		x	x	x	x		810–1820
<i>Boophis boehmei</i>		x					820
<i>Boophis erythrodactylus</i>	x	x					420–830
<i>Boophis luteus</i>	x						400–500
<i>Boophis madagasariensis</i>	x	x					420–820
<i>Boophis majori</i>	x	x	x				420–1120
<i>Boophis reticulatus</i>			x	x			1120–1470
<i>Boophis</i> sp. 2	x						420–440
<i>Boophis</i> sp. 3	x						400–440
<i>Boophis</i> sp. 4		x	x	x			820–1400

TABLE 11-1. *Continued*

Species	Humid forest					Spiny forest	Elevation range (m)
	Site 1 440 m	Site 2 810 m	Site 3 1200 m	Site 4 1500 m	Site 5 1875 m	Site 6 120 m	
REPTILIA							
CHAMAELEONTIDAE							
<i>Brookesia nasus</i>	x	x	x	x	x		410–1920
<i>Calumma brevicornis</i>		x		x	x		810–1890
<i>Calumma capuroni</i>				x	x		1400–1920
<i>Calumma gastrotaenia</i>		x	x	x			810–1670
<i>Calumma nasuta</i>	x	x	x	x	x		400–1900
<i>Calumma oshaughnessyi</i>		x	x	x	x		810–1850
<i>Calumma</i> sp.			x				1110–1140
<i>Furcifer lateralis</i>						x	120
<i>Furcifer verrucosus</i>						x	120
CORDYLIDAE							
<i>Tracheloptychus madagascariensis</i>						x	120
<i>Zonosaurus brygooi</i>	x	x	x				420–1450
<i>Zonosaurus laticaudatus</i>						x	120
GEKKONIDAE							
<i>Blaeseodactylus sakalava</i>						x	120
<i>Geckolepis typica</i>						x	120
<i>Hemidactylus mercatorius</i>						x	120
<i>Lygodactylus miops</i>	x						420–490
<i>Lygodactylus verticellatus</i>						x	120
<i>Lygodactylus montanus</i>					x		1740–1870
<i>Phelsuma mutabilis</i>						x	120
<i>Phelsuma quadriocellata</i>		x					820–850
<i>Phelsuma</i> sp. nov.		x	x		x		810–1940
<i>Paroedura androyensis</i>						x	120
<i>Paroedura bastardi</i>						x	120
<i>Paroedura pictus</i>						x	120
<i>Uroplatus malama</i>			x				1180–1200
<i>Uroplatus malahelo</i>		x	x				850–1200
<i>Uroplatus sikorae</i>	x		x				460–1160
OPLURIDAE							
<i>Chalarodon madagascariensis</i>						x	120
<i>Oplurus cyclurus</i>						x	120
<i>Oplurus quadrimaculatus</i>						x	120
<i>Oplurus saxicola</i>						x	120
SCINCIDAE							
<i>Amphiglossus anosyensis</i>		x					780
<i>Amphiglossus igneocaudatus</i>						x	120
<i>Amphiglossus macrocercus</i>			x				810–1250
<i>Amphiglossus melanopleura</i>	x	x					400–780
<i>Amphiglossus ornaticeps</i>	x	x	x			x	120–1150
<i>Amphiglossus punctatus</i>	x		x				400–1200
<i>Amphiglossus</i> sp.					x		1850
<i>Mabuya aureopunctata</i>						x	120
<i>Mabuya dumasi</i>						x	120
<i>Mabuya elegans</i>						x	120
<i>Mabuya gravenhorstii</i>						x	120
<i>Mabuya vato</i>						x	120
BOIDAE							
<i>Boa dumerilii</i>						x	120
<i>Boa manditra</i>		x					780

TABLE 11-1. *Continued*

Species	Humid forest					Spiny forest	Elevation range (m)
	Site 1 440 m	Site 2 810 m	Site 3 1200 m	Site 4 1500 m	Site 5 1875 m	Site 6 120 m	
COLUBRIDAE							
<i>Dromicodryas bernieri</i>						x	120
<i>Geodipsas infralineata</i>	x		x	x			440–1450
<i>Geodipsas</i> sp. 1	x						420–450
<i>Geodipsas</i> sp. 2				x			1430
<i>Leioheterodon geayi</i>						x	120
<i>Liophidium</i> sp.	x						440
<i>Liopholidophis epistebes</i>	x	x	x				430–1300
<i>Liopholidophis infrasignatus</i>	x						420–440
<i>Liopholidophis pinguis</i>			x		x		1250–1840
<i>Lycodryas betsileanus</i>	x						470
<i>Madagascarophis colubrinus</i>						x	120
<i>Mimophis mahfalensis</i>						x	120
<i>Pseudoxyrhopus sokosoko</i>		x	x				760–1100
<i>Pseudoxyrhopus tritaeniatius</i>			x				1100
TYPHLOPIDAE							
<i>Typhlops decorsei</i>						x	120
<i>Typhlops boettgeri</i>						x	120
Total amphibian species per site	24	29	24	15	5	4	
Total reptile species per site	14	16	18	8	9	30	

Discussion

Parcel 1 (Rain Forest)

Although we are confident that our herpetofaunal survey of parcel 1 is reasonably complete,

we failed to find some species known to occur there, and there are undoubtedly species within the parcel that have yet to be recorded. Andreone and Randriamahazo (1997) surveyed the herpetofauna of lowland rain forest (200–700 m elevation) in parcel 1 in an area southeast

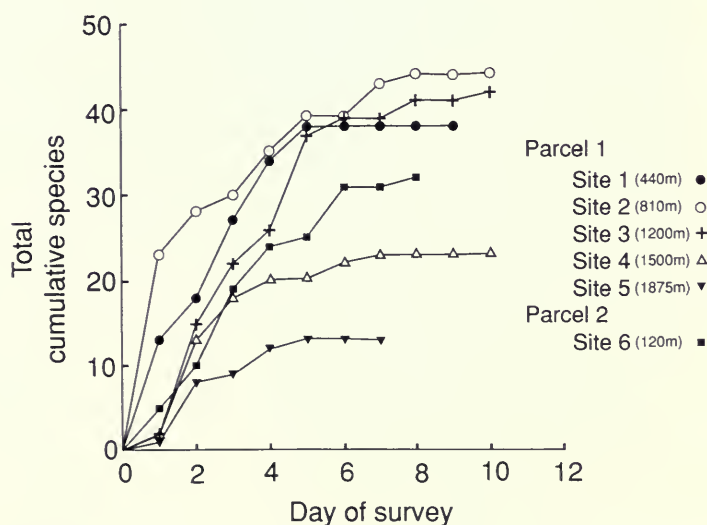


FIG. 11-1. Species accumulation curves for all five localities (sites 1–5) within parcel 1 (rain forest) and parcel 2 (site 6, spiny forest) of the RNI d'Andohahela.

TABLE 11-2. Summary of pitfall positions, trap dates, and capture results for amphibians and reptiles in parcels 1 and 2 of the RNI d'Andohahela.

Line	Topography	Altitude (m)	Start date	End date	Total trap-days	Total captures	Total species	Daily capture success (%)
Parcel 1								
1	V	440	20 Oct	26 Oct	77	9	4	11.7
2	S	440	20 Oct	26 Oct	77	8	5	10.4
3	R	440	20 Oct	26 Oct	77	7	3	9.1
4	V	810	29 Oct	5 Nov	88	2	2	2.3
5	S	810	29 Oct	5 Nov	88	0	0	0
6	R	810	29 Oct	5 Nov	88	3	3	3.4
7	R	1200	7 Nov	15 Nov	99	5	2	5.1
8	V	1200	7 Nov	15 Nov	99	3	2	3.0
9	S	1200	7 Nov	15 Nov	99	3	2	3.0
10	V	1500	17 Nov	25 Nov	99	0	0	0
11	S	1500	18 Nov	25 Nov	88	0	0	0
12	R	1500	18 Nov	25 Nov	88	1	1	1.1
13	V	1875	27 Nov	3 Dec	77	0	0	0
14	R	1875	27 Nov	3 Dec	77	0	0	0
15	S	1875	28 Nov	3 Dec	66	0	0	0
All of parcel 1		440–1875	20 Oct	3 Dec	1,287	41	11	3.2
Parcel 2								
16	S	120	8 Dec	13 Dec	66	1	1	1.5
17	R	120	8 Dec	13 Dec	66	0	0	0
18	V	120	8 Dec	13 Dec	66	3	2	4.5
All of parcel 2		120	8 Dec	13 Dec	198	4	2	2.0
All		120–1875	20 Oct	13 Dec	1,485	45	13	3.0

R = ridge, S = slope, V = valley, F = flat area. Total trap-days = the number of buckets in a line times the number of days the line was in place. Daily capture success is the number of captures divided by the total trap-days.

TABLE 11-3. Amphibian and reptile capture results for all pitfall lines installed within the RNI d'Andohahela.

Species sampled	Number of captures																		Total
	Parcel 1															Parcel 2			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	
AMPHIBIA																			
<i>Mantidactylus boulengeri</i>		2	2	3															7
<i>Mantidactylus decaryi</i>									1										1
<i>Anodonthyla nigrigularis</i>		1																	1
<i>Plethodontohyla bipunctata</i>						1													1
<i>Plethodontohyla inguinalis</i>								1											1
<i>Plethodontohyla laevipes</i>												1							1
<i>Scaphiophryne brevis</i>																1	2		3
<i>Scaphiophryne calcarata</i>																	1		1
REPTILIA																			
<i>Zonosaurus brygooi</i>		1	4	1															6
<i>Amphiglossus macrocerus</i>					1		1	4	2										8
<i>Amphiglossus melanopleura</i>		4	1	3	1														9
<i>Amphiglossus ornaticeps</i>						1													1
<i>Amphiglossus punctatus</i>		1	1				1		2										5

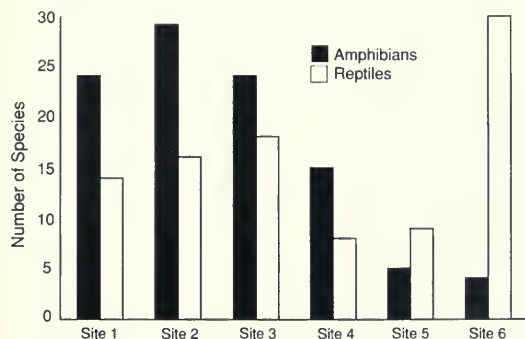


FIG. 11-2. Species diversity of amphibians and reptiles at the five localities (sites 1–5) within parcel 1 (rain forest) and parcel 2 (site 6, spiny scrub forest) of the RNI d'Andohahela.

(46°51.25'E, 24°45.50'S) of our transect between the villages of Isaka-Ivondro and Eminiminy. There is considerable similarity between their results and ours for lowland rain forest. The few differences that exist (Table 11-4) may be explained by (1) different taxonomic interpretations, (2) site differences, (3) temporal differences, and (4) idiosyncratic differences in collecting tech-

niques. Additionally, within parcel 1 our surveys were restricted to primary rain forest. Therefore, widespread species such as *Ptychadena mascareniensis*, *Mabuya gravenhorstii*, and *Oplurus quadrimaculatus* that occur in open and/or disturbed areas were not recorded by us, although they undoubtedly occur at such sites within the RNI d'Andohahela.

Andreone and Randriamahazo (1997) recorded 24 amphibian and 18 reptile species between 200 and 630 m, compared to the 24 amphibian and 14 reptile species we recorded at site 1 (440 m). However, some of the species recorded by Andreone and Randriamahazo were found only in disturbed nonforest habitats, which are abundant at the lower elevation sites they visited. When their records for nonforest species (*Ptychadena mascareniensis*, *Boophis miniatus*, *Oplurus quadrimaculatus*, *Hemidactylus mercatorius*, and *Mabuya gravenhorstii*) are eliminated, their list becomes even more similar to ours for lowland species. Forest species recorded by Andreone and Randriamahazo (1997) but not found by us are *B. difficilis*, *Mantidactylus* cf. *mocquardi*, and *M.* cf. *peracca*, among amphibians, and *Ebenavia in-*

TABLE 11-4. Species reported in low-elevation rain forest (parcel 1) of the RNI d'Andohahela by Andreone and Randriamahazo (1997) that were not recorded by us during the 1995 inventory of the reserve.

Species	Elevation (m)	Forest habitat	Nonforest habitat
AMPHIBIA			
MANTELLIDAE			
<i>Mantidactylus</i> cf. <i>mocquardi</i>	390–610	X	
<i>Mantidactylus</i> cf. <i>peracca</i>	560	X	
RANIDAE			
<i>Ptychadena mascareniensis</i>	200		X
RHACOPHORIDAE			
<i>Boophis difficilis</i>	390–580	X	
<i>Boophis miniatus</i>	200		X
REPTILIA			
CORDYLIDAE			
<i>Zonosaurus</i> cf. <i>madagascariensis</i>	290–320	X	X
GEKKONIDAE			
<i>Ebenavia inunguis</i>	305	X	
<i>Hemidactylus mercatorius</i>	270		X
<i>Paragehyra gabriellae</i>	310–320	X	
OPLURIDAE			
<i>Oplurus quadrimaculatus</i>	200		X
SCINCIDAE			
<i>Mabuya gravenhorstii</i>	270		X
COLUBRIDAE			
<i>Liopholidophis rhadinaea</i>	340	X	

unguis, *Paragehyra gabriellae*, *Zonosaurus* cf. *madagascariensis*, and *Liopholidophis rhadinaea*, among reptiles. In addition, Andreone and Randriamahazo recorded an undetermined species of subfossorial skink, *Amphiglossus* sp., that they believed was either close to *A. ornaticeps* or actually that species. Because we recorded *A. ornaticeps* at several sites within parcel 1, it seems likely that their specimen belongs to the same taxon as ours, regardless of specific identification.

Although we did not find *Mantidactylus mocquardi*, we did record *M. femoralis* at several sites and strongly suspect from the photographs published by Andreone and Randriamahazo (1997, figs. 45, 46) that their specimens are actually *M. femoralis*, a possibility considered by the authors themselves. Similarly, their *Zonosaurus* cf. *madagascariensis* is undoubtedly the same species as our *Z. brygooi*. Individuals of *Z. brygooi* in southern populations, including those in parcel 1, are on average slightly larger and have a more variable number of supralabials anterior to the subocular than individuals of that species in the typical northern populations. This geographical variation may explain why Andreone and Randriamahazo were uncertain about the identity of this form. We did not find *Ebenavia inunguis*, *Paragehyra gabriellae*, and *Liopholidophis rhadinaea* within the reserve, but we have many records of these species from nearby areas and would have expected them to occur in parcel 1. Their *Boophis difficilis* may be the same as one of our three unidentified species of *Boophis*. *Mantidactylus peraccae*, also not recorded by us, is another problematic discrepancy between their list and ours. *Mantidactylus peraccae* is recorded with certainty only from northern Madagascar. Andreone and Randriamahazo (1997) indicated that their specimen from parcel 1, along with others from the Anosyenne Mountains north of Andohahela, is a new species related to *M. peraccae*. Their photograph (1997, fig. 51) of “*M. cf. peraccae*” from parcel 1 is of a species identical to one we collected in 1990 at Ampamakiesiny (UMMZ 198405–11), Manantantely (UMMZ 198403), and in 1991 at Manangotry (UMMZ 198412–3), all of which are localities very close to parcel 1. We identified these specimens as members of a new species, similar to *M. elegans*, that we have not yet described.

In regard to altitudinal distribution, there is only one important discrepancy between the species list of Andreone and Randriamahazo (1997) and our list. They recorded *Mantidactylus bertini*

in low-altitude rain forest (310–580 m), whereas we recorded the species only at higher elevations. In 1990 we recorded it at 580 m (Marosohy) and 800 m (Ampamakiesiny), just north of parcel 1 in the Anosyenne Mountains, and during the present survey we recorded it at 1500 m within parcel 1 (site 4). Only two other species of frog recorded by us in parcel 1 have such a wide elevational range. *Mantidactylus eiselti* was found at sites 1–4 (430–1500 m); if the records by Andreone and Randriamahazo (1997) are considered together with ours for *Boophis andohahela*, the latter species ranges from 300 m to 1820 m within parcel 1.

Undoubtedly there are additional species within parcel 1 that have yet to be recorded. The large heterogeneous rain forests of the region are inadequately explored, and the herpetofauna has yet to be surveyed during the cool dry season, when the activity patterns of some species may change and their detectability increase. Additional surveys, especially at mid- to high elevations in the southern part of parcel 1 and during the cool dry season in all parts of parcel 1, are needed to complete the survey of this crucially important reserve.

Species of amphibians and reptiles that are likely to occur in parcel 1 but have yet to be documented are listed in Table 11-5. This list is based on our large amount of unpublished survey data for surrounding areas and includes species that occur near parcel 1 in the Vohimena and Anosyenne mountains and in the littoral forests near Tolagnaro. Some of these records are reported in Ramanamanjato (1993) and in an unpublished faunal study (1992) presented to QIT FER et Titane, Inc., Montreal, Quebec, Canada. The results of the QIT FER study and many more recent distributional records are documented by specimens in the collections of UMMZ and UADBA.

All of the species listed in Table 11-5, with the exception of *Pseudoxyrhophus microps*, occur at low elevations and either are specialists of open or edge habitats or have wide ecological tolerances that allow them to occur in both lowland rain forest and littoral forest. Many thrive in disturbed habitats, and some are anthropophilic. They are expected to occur at the lower borders of parcel 1 in swampy areas, along open stream corridors, and in abandoned fields and burned areas. *Pseudoxyrhophus microps* is a secretive nocturnal snake that is rarely encountered and may have been missed. No typhlopids were recorded in parcel 1. Typhlopids are secretive burrowing snakes, and the rain forest forms are

TABLE 11-5. Species of amphibians and reptiles likely to occur in parcel 1 of the RNI d'Andohahela that have yet to be recorded there, based on unpublished data from our surveys of nearby rain forest habitat.

Species	Localities near parcel 1
AMPHIBIA	
HYPEROLIIDAE	
<i>Heterixalus boettgeri</i>	Manantantely, Nahampoana; low elevations, open vegetation
MANTELLIDAE	
<i>Mantidactylus grandidieri</i>	Manantantely, Nahampoana, Ampamakiesiny; low-elevation streams
<i>Mantidactylus pulcher</i>	Ampamakiesiny; relatively dry, palm and <i>Pandanus</i> habitats
REPTILIA	
CHAMAELEONTIDAE	
<i>Furcifer lateralis</i>	Many sites; possibly within open/degraded areas at lower elevations
<i>Furcifer verrucosus</i>	Many sites; possibly within open/degraded areas at lower elevations
CORDYLIDAE	
<i>Zonosaurus maximus</i>	Manantantely, Vohimena Mountains, may occur along low-elevation streams within parcel 1
GEKKONIDAE	
<i>Geckolepis maculata</i>	Manantantely and many low-elevation degraded sites
<i>Phelsuma antanosy</i>	Ambatorongorongo, Petriky, Ste. Luce; low-elevation palm forests
<i>Phelsuma lineata</i>	Nahampoana, Manangotry, Ampamakiesiny; low-elevation, rain forest
<i>Phelsuma modesta</i>	Many sites; open, low elevations
COLUBRIDAE	
<i>Langaha madagascariensis</i>	Ambatorongorongo, Manantantely; open/disturbed, dry and mesic forest
<i>Leioheterodon madagascariensis</i>	Ampamakiesiny, surrounding littoral forests; low elevation, open sites
<i>Liophidium rhodogaster</i>	Manantantely, Nahampoana; low-elevation rain forest
<i>Liopholidophis lateralis</i>	Manantantely, Ambatorongorongo; low swampy, open areas
<i>Lycodryas arctifasciatus</i>	Manantantely, Ambatorongorongo; low-elevation rain forest
<i>Lycodryas gaimardi</i>	Manangotry, Ambatorongorongo; low-elevation, open/disturbed sites
<i>Madagascarchophis colubrinus</i>	Manantantely, Nahampoana; low-elevation rain forest
<i>Pseudoxyrhophus microps</i>	Manantantely, Manangotry, Marosohy, Ampamakiesiny; mid-elevations
TYPHLOPIDAE	
<i>Typhlops ocellaris</i>	Manantantely; low-elevation rain forest

among the most difficult species of the Malagasy herpetofauna to detect. It would not be surprising if one or more typhlopids species were found to occur in parcel 1. *Typhlops ocellaris* is the most likely candidate in that we recorded this species in the Vohimena Mountains.

In general, the diversity of both amphibians and reptiles in parcel 1 increases slightly with elevation and then declines (Fig. 11-2), consistent with the pattern detected at other sites in Madagascar (Raxworthy et al., 1998). However, the pattern differs in details between amphibians and reptiles. Amphibian diversity increases between sites 1 (440 m) and 2 (810 m) and then declines steeply, with the lowest diversity at the highest elevation (site 5, 1,875 m). Reptile diversity increases to a maximum at site 3 (1,200 m), declines abruptly at site 4 (1,500 m), and then increases somewhat at site 5. Amphibians are more diverse than reptiles at all sites except site 5. The latter pattern

was also observed in the RNI d'Andringitra (Raxworthy & Nussbaum, 1996a) and in the RS d'Anjanaharibe-Sud (Raxworthy et al., 1998).

Most species are relatively restricted in altitudinal range. Among amphibians, 14 species occur at a single site, nine are restricted to two adjacent altitudinal bands, and 16 occur across three bands (altitudinal range of about 750 m). Only three species (*Mantidactylus eiselti*, *M. femoralis*, and *Boophis andohahela*) span four bands (1,000 m range), and none spans the entire transect of about 1,500 m. Two species of reptiles, *Brookesia nasus* and *Calumma nasuta*, occur at all five elevations, with total altitudinal ranges of 419–1,920 and 400–1,900 m, respectively. Another two chamaeleontids, *C. brevicornis* and *C. oshaughnessyi*, occur at the four higher sites, with an elevational range of about 1,040 m. The colubrid snake *Geodipsas infralineata* ranges from site 1 (440 m) up to site 4 (1500 m).

TABLE 11-6. Coefficients of community (C) (above diagonal) and number of species shared (below diagonal) between sites in parcel 1 of the RNI d'Andohahela.

	Site 1	Site 2	Site 3	Site 4	Site 5
Site 1 (440 m)	—	0.39	0.36	0.07	0.04
Site 2 (810 m)	23	—	0.50	0.19	0.08
Site 3 (1200 m)	21	24	—	0.30	0.16
Site 4 (1500 m)	4	11	15	—	0.37
Site 5 (1875 m)	2	4	8	10	—

C = number of species in common/total species in the two communities being compared.

Coefficients of community (C), or similarity indices, were calculated to examine the change of herpetofaunal species with increasing altitude along the transect within parcel 1 (Table 11-6). As expected, coefficients of community are higher among adjacent elevational bands. The highest coefficient (0.50) is between sites 2 and 3; these are also the two elevational bands with the greatest diversity. Site 1 shares 23 species with site 2 and 21 species with site 3, but only four species with site 4, indicating that a major turnover of species occurs above site 3, or above about 1200 m. Altitudinal zonation of herpetofaunal species has been documented before in Madagascar. Raxworthy and Nussbaum (1994c) reported a marked turnover in species at 900 m in the PN de la Montagne d'Ambre in extreme northern Madagascar. It appears that the highest rate of species turnover may be at a higher elevation (± 1200 m) in parcel 1 of the RNI d'Andohahela.

The species lists for parcel 1 produced by Andreone and Randriamahazo (1997) and the current study yielded few surprises. Most of the species found in parcel 1 had already been recorded in the extreme southeastern region of Madagascar during our earlier studies beginning in 1989 and were partially documented in Ramanamanjato (1993), Raselimanana (1993), and Raxworthy and Nussbaum (1996a). The only two exceptions are the discovery of a new species of rock-dwelling *Phelsuma* and the occurrence of *Pseudoxyrhopus tritaeniat* within the reserve. Previously the southernmost locality for *P. tritaeniat* was within the PN de Ranomanfana (Raxworthy & Nussbaum, 1994a), about 375 km north of the RNI d'Andohahela.

The distinctiveness of the herpetofauna of parcel 1 can be examined by comparing it to the rain forest herpetofaunas of the PN de la Montagne d'Ambre in northern Madagascar (1,300 linear km northeast of parcel 1), the RS d'Anjanaharibe-

Sud in north-central Madagascar (1,070 linear km northeast of parcel 1), and the RNI d'Andringitra in south-central Madagascar (285 linear km northeast of parcel 1). Raxworthy and Nussbaum (1994c) recorded 24 species of amphibians and 46 reptiles in Montagne d'Ambre. Of these, 15 species (seven amphibians and eight reptiles) are shared with parcel 1 (Table 11-7). An additional eight species (one amphibian and seven reptiles) that occur in the rain forests of Montagne d'Ambre also occur near parcel 1 but have yet to be recorded there. Anjanaharibe-Sud, with 53 species of amphibians and 40 reptiles, shares a higher number of species of both amphibians (19) and reptiles (15) with parcel 1. Another three amphibians and three reptiles found at Anjanaharibe-Sud also occur near parcel 1 but have yet to be found within it. Andringitra, with 57 amphibian species and 35 reptiles, shares an even higher number of amphibians (24) with parcel 1 but the same number of reptiles (15) as Anjanaharibe-Sud; this probably reflects the lower total number of reptiles at Andringitra. Three amphibian and three reptile species that occur at Andringitra are found in the Tolagnaro area but have yet to be recorded in parcel 1.

The above considerations show that herpetofaunal similarity between sites, as expected, decreases with distance. It is also apparent that many herpetofaunal species in Madagascar have broad distributions, with the result that parcel 1, as well as most other rain forest sites in Madagascar, does not contain a high percentage of endemic species.

There is only one herpetofaunal species, the new *Phelsuma*, that is apparently endemic to parcel 1. It will probably eventually be found outside of parcel 1. Several additional species are known only from the southern rain forests of the Anosyenne and Vohimena mountains and may be considered southern rain forest endemics. These Anosyenne-Vohimena regional endemics are the mantellid frogs *Mantella haraldmeieri*, *Mantidactylus guibei*, *M. (= Boophis) microtis*, and *M. microtypanum*; the microhylid frogs *Anodonthyla nigrigularis*, *Anodonthyla rouxae*, and *Madecaseophryne truebae*; the chameleontid *Calumma capuroni*; the gekkonid *Paragehyra gabriellae*; and the colubrid *Pseudoxyrhopus sokosoko*.

Montane species found at ≥ 1500 m in parcel 1 include *Mantidactylus elegans*, *M. guibei*, *Amphiglossus* sp., *Calumma capuroni*, and *Lygodactylus montanus*. The restricted distributions of *M. guibei* and *C. capuroni* to high elevations in the southern rain forests and the lack of information

TABLE 11-7. Herpetofaunal species (alphabetical within order) shared between parcel 1 of the RNI d'Andohahela (data from the present study and Andreone & Randriamahazo, 1997, exclusive of the nonforest records reported by the latter authors) and other sites: PN de la Montagne d'Ambre (data from Raxworthy & Nussbaum, 1994c), RS d'Anjanaharibe-Sud (data from Raxworthy et al., 1998), RNI d'Andringitra (Raxworthy & Nussbaum, 1996a).

Species shared by parcel 1 and Montagne d'Ambre	Species shared by parcel 1 and Anjanaharibe-Sud	Species shared by parcel 1 and Andringitra
AMPHIBIA	AMPHIBIA	AMPHIBIA
<i>Aglyptodactylus madagascariensis</i>	<i>Aglyptodactylus madagascariensis</i>	<i>Aglyptodactylus madagascariensis</i>
<i>Boophis luteus</i>	<i>Anodonthyla boulengeri</i>	<i>Anodonthyla boulengeri</i>
<i>Boophis madagascariensis</i>	<i>Boophis albilabris</i>	<i>Boophis albilabris</i>
<i>Boophis miniatus</i>	<i>Boophis albipunctatus</i>	<i>Boophis albipunctatus</i>
<i>Mantidactylus femoralis</i>	<i>Boophis erythrodractylus</i>	<i>Boophis boehmei</i>
<i>Mantidactylus bicalcaratus</i>	<i>Boophis madagascariensis</i>	<i>Boophis luteus</i>
<i>Platypelis grandis</i>	<i>Boophis reticulatus</i>	<i>Boophis madagascariensis</i>
<i>Ptychadena mascareniensis</i> *	<i>Mantidactylus aglavei</i>	<i>Boophis miniatus</i>
	<i>Mantidactylus betsileanus</i>	<i>Boophis reticulatus</i>
REPTILIA	<i>Mantidactylus bicalcaratus</i>	<i>Mantidactylus aglavei</i>
<i>Amphiglossus melanopleura</i>	<i>Mantidactylus biporus</i>	<i>Mantidactylus bertini</i>
<i>Boa manditra</i>	<i>Mantidactylus elegans</i>	<i>Mantidactylus betsileanus</i>
<i>Calumma brevicornis</i>	<i>Mantidactylus femoralis</i>	<i>Mantidactylus bicalcaratus</i>
<i>Calumma nasuta</i>	<i>Mantidactylus luteus</i>	<i>Mantidactylus biporus</i>
<i>Calumma oshaughnessyi</i>	<i>Mantidactylus opiparis</i>	<i>Mantidactylus eiselti</i>
<i>Ebenavia inunguis</i>	<i>Mantidactylus peraccae</i>	<i>Mantidactylus femoralis</i>
<i>Geodipsas infralineata</i>	<i>Mantidactylus ulcerosus</i>	<i>Mantidactylus lugubris</i>
<i>Uroplatus sikorae</i>	<i>Platypelis grandis</i>	<i>Mantidactylus luteus</i>
<i>Geckolepis maculata</i> *	<i>Plethodontohyla laevipes</i>	<i>Mantidactylus opiparis</i>
<i>Leioheterodon madagascariensis</i> *	<i>Mantidactylus grandidieri</i> *	<i>Mantidactylus peraccae</i>
<i>Liophidium rhodogaster</i> *	<i>Mantidactylus pulcher</i> *	<i>Mantidactylus tornieri</i>
<i>Liopholidophis lateralis</i> *	<i>Ptychadena mascareniensis</i> *	<i>Mantidactylus ulcerosus</i>
<i>Lycodryas arcifasciatus</i> *		<i>Plethodontohyla bipunctata</i>

TABLE 11-7. Continued

Species shared by parcel 1 and Montagne d'Ambre	Species shared by parcel 1 and Anjanaharibe-Sud	Species shared by parcel 1 and Andringitra
<i>Phelsuma lineata</i> *	REPTILIA	<i>Plethodontohyla inguinialis</i>
<i>Pseudoxyrhophus microps</i> *	<i>Amphiglossus melanopleura</i>	<i>Manitactylus grandidieri</i> *
	<i>Amphiglossus punctatus</i>	<i>Manitactylus pulcher</i> *
	<i>Boa manditra</i>	<i>Ptychadena mascarensiensis</i> *
	<i>Calumma brevicornis</i>	
	<i>Calumma gastrotaenia</i>	REPTILIA
	<i>Calumma nasuta</i>	<i>Amphiglossus macrocerus</i>
	<i>Ebenavia inunguis</i>	<i>Amphiglossus melanopleura</i>
	<i>Geodipsas infralineata</i>	<i>Amphiglossus punctatus</i>
	<i>Liopholidophis epistebes</i>	<i>Amphiglossus</i> sp.
	<i>Liopholidophis infrasignatus</i>	<i>Brookesia nasus</i>
	<i>Lycodryas betsileanus</i>	<i>Calumma brevicornis</i>
	<i>Mabuya gravenhorstii</i>	<i>Calumma gastrotaenia</i>
	<i>Phelsuma quadriocellata</i>	<i>Calumma nasuta</i>
	<i>Pseudoxyrhophus tritaeniatatus</i>	<i>Calumma oshaughnessyi</i>
	<i>Uroplatus sikorae</i>	<i>Geodipsas infralineata</i>
	<i>Liophidium rhodogaster</i> *	<i>Mabuya gravenhorstii</i>
	<i>Phelsuma lineata</i> *	<i>Liopholidophis epistebes</i>
	<i>Pseudoxyrhophus microps</i> *	<i>Liopholidophis infrasignatus</i>
		<i>Lygodactylus montanius</i>
		<i>Phelsuma quadriocellata</i>
		<i>Amphiglossus anosyensis</i> *
		<i>Liophidium rhodogaster</i> *
		<i>Phelsuma lineata</i> *

* Species recorded both in the northern rain forest site and in the Tolagnaro region near Andohahela, but not yet recorded in parcel 1.

on their likely sister-species currently preclude any biogeographical discussion of these forms. The three remaining species, however, also occur in montane rain forests north of the southern Anosyenne Mountains and are of biogeographical interest.

Mantidactylus elegans is the most widespread of the three. In addition to parcel 1, it has been recorded at high elevations (from south to north) in the RS d'Ivohibe, RNI d'Andringitra, PN de Ranomafana, RS d'Anjanaharibe-Sud, and RNI de Tsaratanana. We found specimens identical to *Amphiglossus* sp. at similarly high elevations on the Andringitra Massif, indicating a historical link between these two sites. The discovery of *Lygodactylus montanus* above 1500 m in parcel 1 also establishes a biogeographical link between the montane forests of the southern Anosyenne Mountains and Andringitra, where we also found this species. It was originally described from the summit (2060 m) of Ivohibe, south of Andringitra and part of the same mountain complex.

Parcel 2 (Spiny Forest)

The relatively great similarities between the herpetofauna of parcel 1 and other rain forest herpetofaunas as far away as 1,300 km (Montagne d'Ambre) stand in stark contrast to the almost total lack of species in common between parcel 1 and parcel 2, the borders of which are just 5 km apart at the nearest point. The differences result from the rain shadow effect of the Anosyenne Mountains. Westward-flowing air masses leave their moisture burden on the eastern slopes of parcel 1, with little moisture remaining for the parched western slopes and lowlands. The result is a dry environment with a mosaic of spiny and deciduous forests and more mesic gallery forests along the water courses.

The species accumulation curve for site 6 (Fig. 11-2) indicates that our survey of parcel 2 was too brief and that some species may have been missed. In fact, there are two amphibian and 24 reptile species (Table 11-8) that one might expect in similar habitats in this region. We recorded some of these additional species in 1990 at Beraketa, only 22 km from site 6 of parcel 2. These include the amphibian *Boophis tephraeomystax* and the following reptiles: *Pyxis arachnoides*, *Geochelone radiata*, *Pelomedusa subrufa*, *Lygodactylus tuberosus*, *Phelsuma modesta*, *Androngo trivittatus*, *Voeltzkowia lineata*, *Heteroliodon oc-*

cipitalis, *Langaha madagascariensis*, *Leioheterodon madagascariensis*, *Leioheterodon modestus*, *Liophidium apperti*, *Liophidium torquatus*, *Liopholidophis lateralis*, and *Lycodryas guentheri*.

There are at least three possible reasons for the greater diversity recorded at Beraketa. First, as mentioned above, the survey period at parcel 2 may have been too brief. Second, there was a larger survey team (four individuals rather than two) at Beraketa. Third, there may have been real differences in the diversity of the two sites at the times of the surveys because of subtle microhabitat differences interacting with random and unknown factors that influence local extinction and colonization.

Additional species were found in the gallery forests of Berenty Reserve, to the west of parcel 2 along the Mandrare River. These include the typhlopoid snake *Ramphotyphlops braminus*, the colubrid snake *Pseudoxyrhopus kely*, and the cordylid lizard *Zonosaurus trilineatus*. Other species typical of habitats represented in parcel 2 but not recorded there during the current survey are listed in Table 11-8.

As currently documented, the herpetofauna of parcel 2 contains no endemic species and is generally representative of the much broader herpetofauna of the Malagasy southwestern deserts.

Conservation

Prior to our survey of parcel 1 of the RNI d'Andohahela, several species of amphibians and reptiles known from southeastern Madagascar were of concern because they were seemingly rare or of commercial (animal trade) interest. These species are threatened with extinction mainly because of habitat destruction, but also because of their potential value in the animal trade. None of these species is currently protected by law, and prior to our survey none was known to occur within reserves.

Foremost among these species of concern were *Mantella haraldmeieri*, *Calumma capuroni*, *Phelsuma antanosy*, *Uroplatus malahelo*, and *U. malalama*. These species were known from few specimens and had been recorded at only a few sites in areas subjected to ongoing habitat destruction, and they are all of commercial interest. Other species of concern because of their limited distribution, but of less commercial interest, are *Paragehyra gabriellae*, *Pseudoxyrhopus kely*, and *P. sokosoko*. With the exceptions of *Phelsuma an-*

TABLE 11-8. Species not recorded in parcel 2 of RNI d'Andohahela but that possibly occur there, based on our unpublished data for similar habitats in southern Madagascar. Records for Manambaro and Tolagnaro are from within the village and city, and not peripheral areas.

Species	Non-RNI d'Andohahela records
AMPHIBIA	
HYPEROLIIDAE	
<i>Heterixalis boettgeri</i>	Tolagnaro, Petriky, Cap Ste. Marie; gallery forests, temporary swamps, and streams
RHACOPHORIDAE	
<i>Boophis tephraeomystax</i>	Beraketa, Tolagnaro, Petriky; gallery forests, temporary swamps, and streams
REPTILIA	
PELOMEDUSIDAE	
<i>Pelomedusa subrufa</i>	Beraketa, many sites in spiny forest; temporary pools and streams
TESTUDINIDAE	
<i>Geochelone radiata</i>	Bereketa; rare in this part of its range
<i>Pyxis arachnoides</i>	Beraketa, Berenty; rare in this part of its range
CORDYLIDAE	
<i>Zonosaurus trilineatus</i>	Berenty, spiny forest near Amboasary-Sud; dense brush
GEKKONIDAE	
<i>Lygodactylus tuberosus</i>	Beraketa, Berenty; open, dry deciduous forests
<i>Phelsuma modesta</i>	Beraketa, Berenty; open forests, relatively dry aspect, disturbed sites
SCINCIDAE	
<i>Amphiglossus splendidus</i>	Bekinana, open slopes of Ambatorongorongo; dry deciduous forests
<i>Androngo trivittatus</i>	Beraketa, Berenty, Petriky, Tolagnaro; spiny and dry deciduous forests, within villages
<i>Voeltzkowia lineata</i>	Beraketa, Petriky; spiny and dry deciduous forests
COLUBRIDAE	
<i>Heteroliodon occipitalis</i>	Beraketa, Berenty, Amboanemba (south of Tranomaro), Cap Ste. Marie; spiny and dry deciduous forest
<i>Ithycyphus oursi</i>	Petriky, Berenty; dry deciduous forest
<i>Langaha madagascariensis</i>	Beraketa, Petriky; dry, often disturbed, spiny and dry deciduous forest
<i>Langaha pseudoalluaudi</i>	Near Amboasary-Sud; spiny forest? Rare, perhaps extinct
<i>Leioheterodon modestus</i>	Beraketa, many sites in SE Madagascar; common in spiny forest
<i>Leioheterodon madagascariensis</i>	Beraketa, many sites in SE; open forests
<i>Liophidium apperti</i>	Beraketa; gallery and spiny forest
<i>Liophidium torquatus</i>	Beraketa, Berenty, many sites in Madagascar, including SE Madagascar; variable habitats
<i>Liophidium vaillanti</i>	Many sites in Madagascar, including SE Madagascar; variable habitats
<i>Liopholidophis lateralis</i>	Beraketa, Petriky, Manambaro, many sites near Tolagnaro; temporary swamps and open areas
<i>Lycodras gaimardi</i>	Petriky, Berenty, many surrounding sites; open areas and lowland forests
<i>Lycodras guentheri</i>	Beraketa; gallery and dry deciduous forests
<i>Pseudoxyrhopus quinquelineatus</i>	Amboanemba (south of Tranomaro); sandy areas in spiny and dry deciduous forests
<i>Pseudoxyrhopus kely</i>	Berenty; littoral and gallery forests, mainly sandy areas
TYPHLOPIDAE	
<i>Ramphotyphlops braminus</i>	Berenty, Manambaro, Petriky, Tolagnaro; sandy areas in a wide variety of habitats including villages, agricultural plots, and gallery forests

tanosy and *Pseudoxyrhopus kely*, all of these species are now known from within parcel 1 of RNI d'Andohahela and are therefore afforded some protection.

In addition, we now know that *Uroplatus malahelo* has a much wider distribution than was previously known. We recorded it at Analavelona near Sakaraha and in RS de Kalambatritra. *Uroplatus malama* is currently recorded from the type locality in the Anosyenne Mountains north of Andohahela, Kalambatritra (unpubl. data), and at one site within Andohahela. Recently discovered specimens of *Uroplatus* in rain forests of northern Madagascar are similar to *U. malama*, but their taxonomic status is uncertain. Although *Paragehyra gabriellae* has not been found outside the Tolagnaro area, it has been recorded at many sites in the vicinity of Andohahela, including Ambatorongorongo, Grand Lavasoa, Manantantely, Vohisandria, and the Anosyenne Mountains, both south and north of parcel 1 of RNI d'Andohahela. *Pseudoxyrhopus sokosoko* is also limited locally but is found at many sites within parcel 1 and in nearby forests. *Pseudoxyrhopus kely* has recently been found in Berenty Reserve and a few other lowland sites near Tolagnaro.

Phelsuma antanosy is perhaps of greatest concern. This species is known from only four sites, three of which are within the proposed mining zone for ilmenite sands along the coastal plains on either side of Tolagnaro. One of these three sites is the type locality, which was cleared for crop and charcoal production 1 year after the species was discovered. The other two localities within the mining zone are small blocks of littoral forest. The fourth site, Forêt de Malahelo, on the west slope of Ambatorongorongo, is outside the mining zone just a few kilometers west of the type locality. The west slope of Ambatorongorongo, also the type locality of *Uroplatus malahelo*, had a small patch of degraded, low-elevation rain forest as of 1995, but the forest was being selectively cut for wood, and the annual burning of the surrounding grasslands was destroying 3–10 m of the peripheral forest of Ambatorongorongo each year. Unless action is taken, the forest will be completely eliminated within a few years. *Phelsuma antanosy* was not found in parcel 1 of the RNI d'Andohahela. The species is not easily detected, however, and a concerted effort is needed to determine whether it occurs in some of the lower elevation forests of parcel 1 or in surrounding forests.

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Chapter 12

Bird Community Variation with Elevation and Habitat in Parcels 1 and 2 of the Réserve Naturelle Intégrale d'Andohahela, Madagascar

A. F. A. Hawkins¹ and Steven M. Goodman²

Abstract

A study conducted between 19 October and 14 December 1995 in the Réserve Naturelle Intégrale d'Andohahela, southeastern Madagascar, found 123 species of birds, a high total for a small (<700 km²) area. This high species richness was due to the variety of habitats sampled: humid forest from 400 to 1875 m, spiny forest, and open areas. Of these the lowland humid forest is considered to be the highest priority for bird conservation management. The bird community in the humid forest sample was relatively homogeneous, with a low turnover rate corresponding to changes in altitude; only 14 of 50 species, however, were found evenly over the elevational gradient. Species richness was slightly greater at mid-elevation and lower at high elevation. Species richness estimates within elevational zones were found to be distorted unrealistically by compensation for sampling area. This was because most sampling sites within an elevational sample shared the same species. The bird community in the spiny forest was very different from that in the humid forest; of 86 forest species found in all habitats, only 26 occurred in both humid and spiny forest. Raptors and frugivores made up a disproportionately large part of these 26 species, whereas small insectivores were underrepresented.

Résumé

Une étude conduite entre 19 octobre et 14 décembre 1995 dans la Réserve Naturelle Intégrale d'Andohahela a permis de déceler 123 espèces d'oiseaux, une proportion élevée pour une petite étendue de Madagascar. Ceci peut s'expliquer par la variété d'habitats sélectionnée comme échantillons: forêt humide comprise entre 400 m et 1875 m d'altitude, forêt sèche, et des zones ouvert. La forêt humide de basse altitude est considérée comme la priorité la plus pressante en matière de gestion de conservation. La communauté d'oiseaux rencontrée à l'intérieur de l'échantillon de forêt humide est relativement homogène, avec un taux d'apparition de plus en plus faible en montant en altitude; toutefois 14 espèces seulement sur 50 sont rencontrées régulièrement sur une pente de même altitude. La richesse en espèce est légèrement plus élevée en moyenne altitude, moins élevée à haute altitude. Les estimations en richesse en cette espèce selon les niveaux d'altitude s'avèrent erronées si on se base aux zones d'échantillonnage, étant donné que la plupart des sites d'échantillonnage sur une altitude déterminée renferment les mêmes espèces. La communauté d'oiseaux dans la forêt sèche est très différente; sur toutes les 86 espèces identifiées, 26 seulement apparaissent dans la forêt humide ainsi que dans la forêt

¹ BirdLife International, B.P. 1074, Antananarivo (101), Madagascar.

² Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, IL 60605-2496, U.S.A.

sèche. Les rapaces et frugivores composent une partie disproportionnée de ces 26 espèces. Les petits insectivores sont sous-représentés.

Introduction

The Réserve Naturelle Intégrale (RNI) d'Andohahela, with its three disjunct parcels (see Chapter 1), is unusual in comparison to most protected areas of Madagascar in that it encompasses a remarkable variety of habitats within a single reserve. These habitats include the humid forest and high mountain zones of parcel 1, the spiny forest and remnant gallery forest of parcel 2, and the transitional zone between humid and spiny forest of parcel 3. The abrupt ecotones between the parcels are reflected in dramatic changes in the bird species inhabiting them. A recently published monograph on the birds of southeastern Madagascar included ornithological information from the 1995 survey of the RNI d'Andohahela and earlier research conducted in the reserve as well as surrounding areas (Goodman et al., 1997). One of the analyses presented in that study shows high levels of species turnover between the parcels. The bird fauna of the eastern humid forest of Madagascar, a region extending nearly 1,200 km between parcel 1 of the RNI d'Andohahela and the northernmost site it was compared to, is more homogeneous than the bird population found in parcels 1 and 2 of the RNI d'Andohahela, which are separated by a few kilometers. In this chapter we concentrate on the Andohahela region, review information on the elevational distribution of birds in the reserve, examine species turnover between five different elevational zones in the humid forest of parcel 1 and the single site studied in the spiny forest of parcel 2, and provide estimates of densities for certain species. Data on the bird species in parcel 3 are not extensive, and we limit our comparisons to parcels 1 and 2. For additional details on the natural history of bird species that occur within the reserve, see Goodman et al. (1997).

Materials and Methods

Data were collected within a survey area of ± 100 m in elevation and less than 3 km in horizontal distance from survey area centers (= camps) established at 440, 810, 1200, 1500, and 1875 m in the humid forest of parcel 1, and at

120 m in the spiny forest of parcel 2. Species lists were compiled by direct observation while observers walked along forest trails, by call-play-back of bird vocalizations using a tape recorder, from static observations made from broken-canopy watch points, and by mist-netting. Specific details on procedures associated with static observation and mist-netting and their results are given in Goodman et al. (1997).

Point counts were made at 150 m intervals (in humid forest) or 200 m intervals (in spiny forest) along marked and measured preexisting and newly cut forest trails. A minimum of 12 point count sites were sampled within each elevational zone. Where possible a minimum of five point count sites were established within each zone in habitat in each of the following locations: ridge, slope, and valley bottom.

Each point count site was sampled twice, on different days, once between 0430 and 0600 hr and once between 0630 and 0900 hr. During each sample count, which lasted for 10 minutes, the following data were noted on each bird contact: species, estimated distance from observer (to nearest 10 m), nature of initial contact (song, call, wing-noise, or visual), and time of contact. This methodology differs slightly from that used in other inventories (Goodman & Putnam, 1996; Hawkins et al., 1998); findings of previous surveys (Hawkins et al., 1998) indicated that where many (up to five) repeat samples of fewer point count sites were made, much of the data obtained was unusable for density calculations because a large percentage of contacts could not be regarded as statistically independent. In the present survey an effort was made to obtain the largest number of independent samples possible within an elevational zone. Sampling thoroughness for each elevational zone was assessed by examination of species accumulation curves. These curves were calculated based on the day that a species was first detected.

It would be possible to evaluate changes in bird species richness with elevation in the humid forest sites by simply using the number of species within each zone. However, this approach does not take into account varying sampling effort, particularly with regard to the surface area sampled. A potential solution is to compare the logarithm of the

surface area sampled (the number of point counts made at an elevational sample is used here as an index of area sampled) with the logarithm of species richness (Rahbek, 1995). An alternative method is to standardize and compare the number of species recorded within an elevational zone over a similar number of samples or days.

Species recorded in parcel 1 were scored as occurring in one of five elevational categories according to their presence and relative abundance at sample sites. Species occurring only at 440 and 810 m were classified as lowland species, those occurring only between 440 and 1200 m as low-to mid-elevation species, those occurring only between 810 and 1500 m as mid-elevation species, those only between 810 and 1875 m as mid- to high-elevation species, and those occurring only between 1200 and 1875 m as high-elevation species. Species occurring more or less equally at all sites were considered generalists. Species abundance within an elevational zone was derived from contact frequency on point counts. For some species that rarely vocalized or vocalized quietly (e.g., *Philepitta castanea* and *Pseudobias wardi*), casual contacts revealed that the species was clearly more abundant than contacts on point counts indicated. In these cases the elevational category was adjusted accordingly. Species noted only once within an elevational zone were not considered to occur regularly at that elevation. Only species falling clearly into the elevational categories described above were used in the subsequent analysis.

To assess the relationships between bird communities in sample sites within the reserve, we calculated the Jaccard Index of similarity for the distribution of breeding bird species:

$$\text{Jaccard Index} = \frac{C}{N1 + N2 - C}$$

where N1 = the number of species at site 1, N2 = the number of species at site 2, and C = the number of species common to both sites. The coefficients from these indices were used in a cluster algorithm ("Phylip," written by J. Felsenstein using the Fitch-Margoliash method).

The computer program DISTANCE (Laake et al., 1993) was used to calculate density estimates for species where sufficient independent contacts (18 per elevational zone) were made. For each species, the highest of the two counts made at each point count site was used. Several species for which the number of contacts was relatively high were excluded from the analysis because

most contacts with these species (*Cuculus rochii*, *Coracopsis* spp., and *Leptosomus discolor*) occurred at an estimated distance of more than 200 m. Such data produce very unreliable density estimates (Hawkins et al., 1998) owing to the difficulty of estimating comparatively long distances correctly (Buckland et al., 1993).

Results

One hundred twenty-three bird species were recorded during the survey (Table 12-1). This is an exceptionally high figure for a small geographical area of Madagascar and reflects the diversity of habitats sampled—low-, mid-, and high-elevation humid forest; spiny forest; gallery forest; savanna; and riverine habitats. In parcel 1 a total of 59 species were recorded in the 440 m zone, 64 in the 810 m zone, 63 in the 1200 m zone, 47 in the 1500 m zone, and 38 in the 1875 m zone; there were 81 species recorded at 120 m in parcel 2. The ratios of species within these zones utilizing forest and mixed forest/open habitats to those occurring in open and aquatic habitats were 10.8, 9.8, 11.4, 46.0, 8.3, and 1.3, respectively. It is thus clear that one of the main differences between the bird faunas of parcel 1 and parcel 2 is the much higher percentage of species using open and aquatic habitats in parcel 2. The site surveyed in parcel 2 was adjacent to a tributary of the Mandrare River and areas of aquatic habitat, including a relatively slow-moving river and marshes. These biotopes were largely not present in the various zones surveyed in parcel 1. The percentage of forest and mixed-habitat birds was similar at all humid forest sites below 1875 m (Table 12-1). The percentage of forest species was lower at 1875 m. This reflects the presence of a more or less constant number of aerial species (those that forage in the air outside the forest body) over the whole elevational gradient. Aerial species, as well as numerous open habitat species, make up a higher proportion of the total in the species-poor summit area.

Sampling effort varied in parcel 1 from 12 point counts at 1875 m to 21 at 810 m (Table 12-1). The steepness of slopes, particularly at the 1200 m and 1875 m sites, reduced the potential for increasing sample size. On the basis of the species accumulation curves (Fig. 12-1), more than 90% of the species likely to be present at a site were recorded within the first 3–5 days.

TABLE 12-1. Numbers of species, forest species, and species restricted to a sampling site for all sampling sites in this study of the RNI d'Andohahela.

Descriptive parameter	Humid forest sites (parcel 1)					Spiny forest (parcel 2)	Total
	440 m	810 m	1200 m	1500 m	1875 m		
Days of survey effort	10	10	10	9	7	9	55
Number of point count sites	17	21	15	20	12	28	113
Number of bird species	59	64	63	47	38	81	123
Number of forest bird species (% of total)	57 (97)	61 (95)	60 (95)	47 (100)	31 (82)	50 (62)	86 (69)
Percentage of species recorded on point counts	64	70	78	78	79	—	—
Number of bird species restricted to that site	5	1	1	1	1	40	—

The humid forest sites can be divided into two groups (species-poor and species-rich) based on the number of species present (Fig. 12-2A). Despite the disparity in the number of point count sites sampled in the 440, 810, and 1200 m samples, the number of species present within each is similar. The two high-elevation sites have distinctly fewer species. Of the humid forest sites sampled, the 440 m zone had by far the largest number of unique species (five; Table 12-2). All other elevational zones shared almost all species with at least one other zone.

Biogeography

Given the differences in the number of species in open and forested habitats between the two par-

cels, the Jaccard Index has been calculated in two ways: for the overall avifauna and for species that occur only in forested and mixed habitats. Analysis of the complete avifauna in the five surveyed zones in parcel 1 and the single study site in parcel 2 (Table 12-2; Fig. 12-3A) indicates that the sites within parcel 1 form a distinct cluster. Within these sites the 810 m and 1200 m zones have a very similar avifauna forming the upper lowland and mid-montane community; these zones are then next closest in faunal similarity to 440 m, followed by 1500 m, and then finally 1875 m. Parcel 2 has a distinctly different avifauna than the humid forest sites. On the basis of this analysis the spiny forest parcel has an avifauna closest to that of the high mountain site in humid forest, at 1875 m.

When the analysis is repeated without the

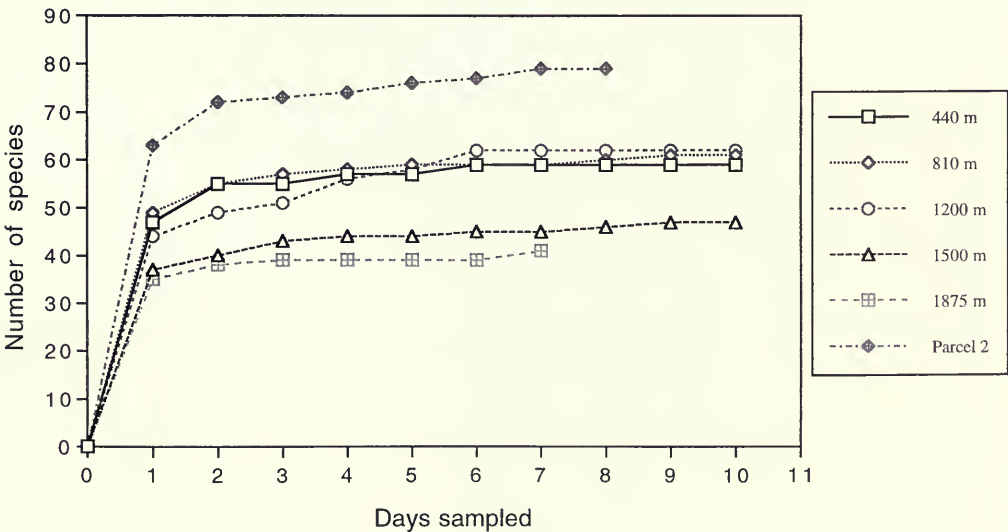


FIG. 12-1. Species accumulation curves for the five elevational zones in humid forest of parcel 1 and the spiny forest of parcel 2 in the RNI d'Andohahela.

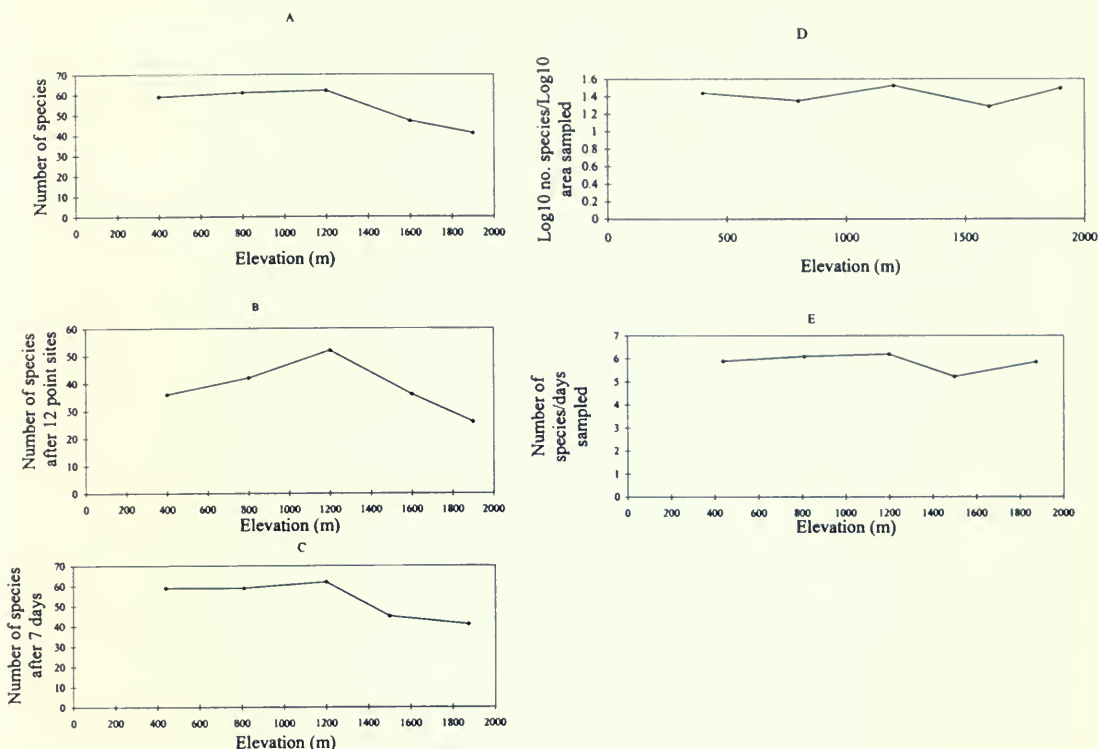


FIG. 12-2. The number of species recorded within each elevational zone in humid forest in the RNI d'Andohahela as measured by all techniques combined (A), after 12 point counts (B), after 7 days of sampling using all techniques combined (C), as adjusted for surface area sampled (D; Rahbek, 1995), and total number of species recorded by all methods adjusted for the number of survey days (E).

aquatic, open habitat, and aerial species, the same basic pattern exists (Fig. 12-3B). The only subtle difference with the latter analysis is that the distances between nodes within the 440, 810, 1200, and 1500 m cluster are smaller, whereas the 1875 m site is further from the lower humid forest sites.

Methodological Considerations

In this section we consider the relationships between elevation and species richness and we compare methods of adjusting for sampling effort. Except where stated, the total number of species recorded at a sample site is used. The relationship between elevational zones and unadjusted species richness is illustrated in Figure 12-2A. A similar relationship is shown if sampling time is kept constant (7 days), because of the low number of previously unrecorded species occurring within each elevational zone after 7 days (Fig. 12-2C). If an adjustment is made for area sampled following the method of Rahbek (1995; Fig. 12-2D), however,

sites with fewer samples (1200 m and 1875 m) come out as much more species-rich (Fig. 12-2B).

When sample size is controlled for by dividing the number of species recorded in each zone by the number of days of sampling (as an index of sampling effort; Fig. 12-2E), the results are similar to those shown in Figure 12-2A. Again, the sampling zones with lower effort (particularly 1875 m) come out as more species-rich than in the unadjusted analysis.

Controlling for sample size by taking the number of species discovered using a fixed number of point count sites (12, the minimum at any site; Fig. 12-2B) produces a result similar to that of the unadjusted analysis (Fig. 12-2A), with the exception that the lower elevational zones come out as rather species-poor. This is due to the lower percentages of the total number of species present at 440 m and 810 m that were recorded on point counts (Table 12-1). The species accumulation curves for each elevational zone (Fig. 12-4) show that the general pattern occurs because species

TABLE 12-2. Presence of bird species within elevational zones in the RNI d'Andohahela.

Species	Status	Parcel 1					Else- where in parcel 1	Elevational category	Parcel 2
		440 m	810 m	1200 m	1500 m	1875 m			
<i>Phalacrocorax africanus</i>	N								+
<i>Nycticorax nycticorax</i>	N								+
<i>Ardeola ralloides</i>	N								+
<i>Ardeola idae</i>	*								+
<i>Bubulcus ibis</i>	N								+
<i>Butorides striatus</i>	N								+
<i>Egretta ardesiaca</i>	N								+
<i>Egretta dimorpha</i>	(*)								+
<i>Egretta alba</i>	N								+
<i>Ardea purpurea</i>	N								+
<i>Ardea cinerea</i>	N								+
<i>Scopus umbretta</i>	N								+
<i>Lophotibis cristata</i> #	*	+	+					L-M	
<i>Dendrocygna bicolor</i>	N								+
<i>Dendrocygna viduata</i>	N								+
<i>Sarkidiornis melanotos</i>	N								+
<i>Anas erythrorhyncha</i>	N								+
<i>Aviceda madagascariensis</i> #	*		+						+
<i>Milvus migrans</i>	N								+
<i>Polyboroides radiatus</i> #	*						+		+
<i>Accipiter henstii</i> #	*	+	+					L-M	
<i>Accipiter francesii</i> #	(*)	+	+		+			?G	+
<i>Buteo brachypterus</i> #	*	1	3	1	2	+		G	+
<i>Falco newtoni</i>	(*)						+		+
<i>Falco zoniventris</i>	*								+
<i>Falco eleonorae</i>	M								+
<i>Falco concolor</i>	M								+
<i>Margaroperdix madagascariensis</i>	*						+		
<i>Numida meleagris</i>	I								+
<i>Turnix nigricollis</i> #	(*)						+		5
<i>Dryolimnas cuvieri</i>	(*)	+							2
<i>Canirallus kioloides</i> #	*	+	+	1		2		G	
<i>Sarothrura insularis</i> #	*		+	+	+			?M	
<i>Gallinula chloropus</i>	N								+
<i>Tringa nebularia</i>	M								+
<i>Actitis hypoleuca</i>	M								+
<i>Pterocles personatus</i>	*								+
<i>Streptopelia picturata</i> #	(*)	1	6	3	16	4		G	14
<i>Oena capensis</i>	N								+
<i>Treron australis</i> #	(*)	+						L	+
<i>Alectroenas madagascariensis</i> #	*	+	1	+	+	+		G	
<i>Coracopsis vasa</i> #	(*)	4	1	2	7	1		?G	9
<i>Coracopsis nigra</i> #	(*)	7	17	16	22	15		G	8
<i>Agapornis cana</i> #	*								6
<i>Cuculus rochii</i> #	(*)	25	30	23	15	+		L-M	28
<i>Coua gigas</i> #	*								16
<i>Coua reynaudii</i> #	*	1	2	5	10	6		?M-H	
<i>Coua cursor</i> #	*								9
<i>Coua ruficeps</i> #	*								20
<i>Coua caerulea</i> #	*	6	12	6	4	2		G	
<i>Coua cristata</i> #	*								18
<i>Centropus toulou</i> #	(*)	3	0	5	2			L-M	29
<i>Otus rutilus</i> #	(*)	+	+	+	+			L-M	+

TABLE 12-2. *Continued.*

Species	Status	Parcel 1					Else- where in parcel 1	Elevational category	Parcel 2
		440 m	810 m	1200 m	1500 m	1875 m			
<i>Ninox superciliaris</i> #	*								+
<i>Asio madagascariensis</i> #	*	+	+	+				L-M	
<i>Caprimulgus</i> <i> madagascariensis</i> #	(*)								+
<i>Caprimulgus enarratus</i> #	*						+		
<i>Zoonavena grandidieri</i> #	(*)	1	1	+		+			+
<i>Cypsiurus parvus</i>	N	+	+	+					+
<i>Apus melba</i>	N	+	+	+		+			+
<i>Apus barbatus</i>	N	+	+	+	+	+			+
<i>Alcedo vintsioides</i>	(*)	+	+						+
<i>Ispidina</i> <i> madagascariensis</i> #	*	+	+	+				L-M	
<i>Merops superciliosus</i>	N						+		+
<i>Eurystomus glaucurus</i>	N				+				5
<i>Brachypteracias</i> <i> leptosomus</i> #	*	3	1	5	+			L-M	
<i>Brachypteracias</i> <i> squamiger</i> #	*	1						L	
<i>Atelornis pittoides</i> #	*			6				M	
<i>Atelornis crossleyi</i> #	*			10	17	2		M-H	
<i>Leptosomus discolor</i> #	*	3	9	5	4	4		G	5
<i>Upupa epops</i> #	N								1
<i>Philepitta castanea</i> #	*	+	1	1	2	+		G	
<i>Neodrepanis coruscans</i> #	*		9	4				M	
<i>Neodrepanis hypoxantha</i> #	*			+	8	9		H	
<i>Mirafra hova</i>	*						+		14
<i>Riparia paludicola</i>	*						+		
<i>Phedina borbonica</i>	*		+	+		+			+
<i>Motacilla flaviventris</i>	*	+	+	+		+			
<i>Coracina cinerea</i> #	*	2	6	3	3	2		G	+
<i>Phyllastrephus</i> <i> madagascariensis</i> #	*	22	19	3				L-M	
<i>Phyllastrephus</i> <i> zosterops</i> #	*	15	9	4				L-M	
<i>Phyllastrephus</i> <i> cinereiceps</i> #	*		+	4	3	5		M-H	
<i>Hypsipetes</i> <i> madagascariensis</i> #	*	17	22	5	3	+		L-M	23
<i>Copsychus</i> <i> albospecularis</i> #	*	7	12	3				L-M	24
<i>Saxicola torquata</i> #	*						+		
<i>Pseudocossyphus sharpei</i> #	*		+	10	13	8		M-H	
<i>Acrocephalus newtoni</i>	*								+
<i>Nesillas typica</i> #	*		7	12	22	23		M-H	
<i>Thamnornis chloropetoides</i> #	*								9
<i>Cisticola cherina</i>	(*)						+		+
<i>Dromaeocercus bruneus</i> #	*			3	3	5		M-H	
<i>Randia pseudozosterops</i> #	*	14	10	1	2			L-M	
<i>Newtonia amphichroa</i> #	*		5	14	8	5		M-H	
<i>Newtonia archboldi</i> #	*								7
<i>Newtonia brunneicauda</i> #	*	11	16	8	12	10		G	38
<i>Newtonia fanovanae</i> #	*	7						L	
<i>Neomixis tenella</i> #	*	23	12	4				L-M	23
<i>Neomixis viridis</i> #	*	6	16	11	10	8		G	
<i>Neomixis striatigula</i> #	*	17	22	8	3			L-M	18

TABLE 12-2. *Continued.*

Species	Status	Parcel 1					Else- where in parcel 1	Elevational category	Parcel 2
		440 m	810 m	1200 m	1500 m	1875 m			
<i>Cryptosylvicola randrianasoloi</i> #	*		2	12	22	11		M-H	
<i>Hartertula flavoviridis</i> #	*	+	2	1	+			?M	
<i>Pseudobias wardi</i> #	*	+	+	2	+			L-M	
<i>Terpsiphone mutata</i> #	*	13	14	2	3			L-M	23
<i>Oxylabes madagascariensis</i> #	*	+	5	3	+	1		?G	
<i>Crossleyia xanthophrys</i> #	*		2	1	6	1		M-H	
<i>Mystacornis crossleyi</i> #	*	2	3	2	3			L-M	
<i>Nectarinia souimanga</i> #	(*)	10	22	16	27	26		G	18
<i>Nectarinia notata</i> #	*	1	1	1				L-M	4
<i>Zosterops maderaspatana</i> #	(*)	20	25	11	15	11		G	1
<i>Calicalicus madagascariensis</i> #	*	16	10	4	5			L-M	
<i>Schetba rufa</i> #	*	6	2					L	
<i>Vanga curvirostris</i> #	*	3		1				?L-M	16
<i>Xenopirostris xenopirostris</i> #	*								5
<i>Xenopirostris polleni</i> #	*		5	8	4	3		M-H	
<i>Falculea palliata</i> #	*								12
<i>Leptopterus viridis</i> #	*	3	7	9	4			L-M	11
<i>Leptopterus chabert</i> #	*	+	3	+				?L-M	2
<i>Cyanolanius madagascarinus</i> #	(*)	9	3	5	2			L-M	
<i>Hypsositta corallirostris</i> #	*	+						L	
<i>Tylas eduardi</i> #	*	18	17	11	5	1		L-M	
<i>Dicrurus forficatus</i> #	*	11	7	6	+	+		L-M	23
<i>Corvus albus</i> #	N								+
<i>Hartlaubius auratus</i> #	*	1	3	+				L-M	
<i>Acridotheres tristis</i>	I								+
<i>Ploceus nelicourvi</i> #	*	1	5	+	2	+		G	
<i>Ploceus sakalava</i> #	*								7
<i>Foudia omisa</i> #	*	1	7	9	17	5		M-H	
<i>Foudia madagascariensis</i> #	(*)					+		?H	14
<i>Lonchura nana</i>	*								+

Species are listed under "Elsewhere in parcel 1" only if they were seen outside the elevational zones. The numerals indicate number of independent contacts with a species from point counts. A plus symbol (+) indicates that the species was recorded within an elevational sample but not on point counts. The pound (#) symbol indicates a species that feeds or breeds regularly in native forest. Under the heading "Status": N = nonendemic resident breeder in Madagascar; * = Malagasy resident breeder; (*) = Malagasy regional endemic breeder; M = migrant nonbreeding visitor; I = introduced. Under the heading "Elevational category," only humid forest (parcel 1) species are analyzed: L = lowland species; L-M = low- to mid-elevation species; M = mid-elevation species; M-H = mid- and high-elevation species; H = high-elevation species; G = elevational generalist.

were recorded at a faster rate over a series of point count sites in species-rich elevational zones.

Species Densities

Density estimates for certain bird species in parcel 1 of the RNI d'Andohahela are presented

in Table 12-3. The calculated densities do not show any marked variation with elevation except in the cases of *Nesillas typica* and *Nectarinia souimanga*, both of which appear to be more common at 1875 m than elsewhere. The species listed in Table 12-3 are less abundant at other altitudes, where frequency of contact was too low for density calculation.

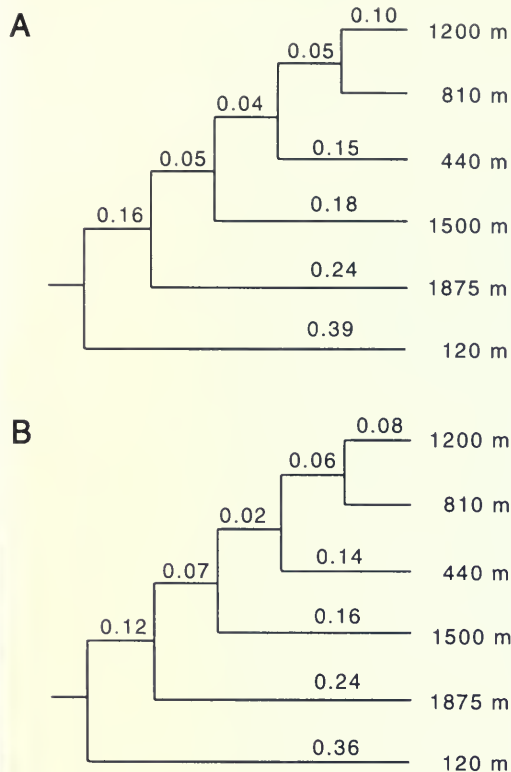


FIG. 12-3. Cluster analysis of faunal similarity of the resident avifauna of the sites surveyed in the RNI d'Andohahela. The coefficients were derived from the Jaccard Index for the general resident bird community (A) and restricted to forest-dwelling species (B). See text (p. 177) for definition of the Jaccard Index.

Discussion

Biogeography

The bird community in the humid forest (parcel 1) of RNI d'Andohahela is relatively homogeneous, and there are no clear abrupt shifts in the species that occur between 440 and 1500 m. At a finer level of analysis the species in the 810 and 1200 m zones are more similar to one another than they are to those in the 440 m zone. This is the result of a few lowland species (e.g., *Treron australis*, *Brachypteracias squamiger*, *Newtonia fanovanae*, and *Hypositta corallirostris*) being confined to the 440 m zone. As one moves up the slopes into the 1500 and 1875 m zones, there is a decrease in similarity, but the Jaccard Index coefficients between these two zones in both analyses are close to 0.60. The dramatic shift in habitats between parcel 1 and parcel 2 is mirrored by

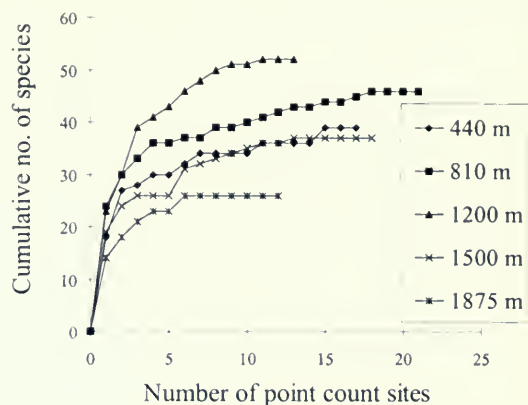


FIG. 12-4. Species accumulation curves based on point counts for each elevational zone.

a change in the avifaunal community. The bird community of parcel 2 is more similar to that in the 1875 m zone of parcel 1 than to any other site along the slopes of the humid forest of the reserve. Insofar as the humid forest in parcel 1 of the reserve ends abruptly along the western flank of the Anosyenne Mountains and the spiny forest habitat is geographically closer to the 1875 m site than most of the other sites surveyed in parcel 1, the faunistic relationship between the 1875 m zone and parcel 2 might simply reflect the ability of certain species to move between these habitats.

Species Distributions

Most humid forest species for which sufficient data are available are either elevational generalists or became more scarce above 1500 m. Five species were limited to lowland, 20 to lowland or mid-elevation, three to mid-elevation, seven to mid- to high elevation, three to high elevation, and 14 were elevational generalists. Thus, few species were completely restricted to the lowland or montane habitats. Of the 50 species for which there were enough data to permit analysis, 72% (36 of 50) showed clear elevational limits. Overall, 23 species (63% of elevation-restricted species) were not recorded at higher elevations, whereas 10 species (27%) were not found in lowland samples.

A striking feature of this study is the abundance of frugivorous species at 1500 m (Table 12-2)—there were considerably higher numbers of two pigeons (*Streptopelia picturata* and *Alectroenas madagascariensis*) and both *Coracopsis* parrots in

TABLE 12-3. Densities of species in the RNI d'Andohahela with more than 18 contacts per elevational zone, with certain exceptions (see text, p. 177).

Species (Elevation)	Mean density estimate (birds/km ²)	Lower 95% confidence interval (birds/km ²)	Upper 95% confidence interval (birds/km ²)	Percentage coefficient of variation	Degrees of freedom
<i>Atelornis crossleyi</i> (1500 m)	67.6	34.8	131.4	33	30
<i>Neomixis tenella</i> (440 m)	436.9	337.2	566.0	12.7	27
<i>Cryptosylvicola randrianansoloi</i> (1500 m)	119.5	68.5	208.5	27.9	34
<i>Phyllastrephus madagascariensis</i> (440 m)	214.3	132.9	345.5	24.1	48
<i>Phyllastrephus madagascariensis</i> (810 m)	156.9	94.5	260.5	24.1	48
<i>Nesillas typica</i> (1500 m)	792.0	503.8	1,245.2	22.8	51
<i>Nesillas typica</i> (1875 m)	1,265.1	855.5	1,870.9	19.7	48
<i>Zosterops maderaspatana</i> (440 m)	688.2	416.7	1,136.7	25.2	38
<i>Zosterops maderaspatana</i> (810 m)	607.8	408.2	905.0	20.1	63
<i>Nectarinia souimanga</i> (810 m)	305.5	222.4	419.9	16.1	80
<i>Nectarinia souimanga</i> (1200 m)	291.7	213.7	398.2	15.7	67
<i>Nectarinia souimanga</i> (1500 m)	393.8	283.6	546.7	16.6	71
<i>Nectarinia souimanga</i> (1875 m)	631.9	485.5	822.5	13.4	97
<i>Tylas eduardi</i> (440 m)	124.1	77.1	199.7	24.1	55

Densities were calculated with the computer program DISTANCE (Laake et al., 1993) from data collected during point counts.

this zone than elsewhere in parcel 1 (the abundance of *Alectroenas madagascariensis* was estimated from casual encounters). This may have been due to the large numbers of fruiting trees at this altitude, but there is no botanical evidence to support such a speculation (see Chapter 4). On casual inspection there appear to be no other obvious or significant relationships between elevational distribution and dietary preference (Table 12-2).

The forest species present in the spiny forest in parcel 2 are markedly different from those in the humid forest. Of a total of 86 forest species for the combined samples, only 26 occurred in both dry and humid forest. These included four raptors (*Aviceda madagascariensis*, *Polyboroides radiatus*, *Accipiter francesii*, *Buteo brachypterus*), three larger frugivores (the two species of *Coracopsis* and *Streptopelia picturata*), one owl (*Otus rutilus*), six large sally-gleaning or gleaning insectivores (*Cuculus rochii*, *Leptosomus discolor*, *Coracina cinerea*, *Vanga curvirostris*, *Leptopterus viridis*, and *Dicrurus forficatus*), four small sally-gleaning or sallying insectivores (*Neomixis tenella*, *N. striatigula*, *Newtonia brunneicauda* and *Terpsiphone mutata*), two insectivore/nectarivores (two species of *Nectarinia*), one terrestrial insectivore (*Copsychus albospectularis*), and three small frugivore/granivores (*Hypsipetes madagascariensis*, *Zosterops maderaspatana*, and *Foudia madagascariensis*). Absent or underrepresented on this list are the bark-feeders and terrestrial in-

sectivores. Frugivores and raptors appear to be overrepresented.

Of the 26 forest species common to the two habitats, at least nine (*Coracopsis vasa*, *C. nigra*, *Coracina cinerea*, *Copsychus albospectularis*, *Neomixis tenella*, *N. striatigula*, *Nectarinia souimanga*, *Vanga curvirostris*, and *Leptopterus viridis*) occur in the different parcels as distinct subspecies (Goodman et al., 1997). In addition, *Otus rutilus* populations in the two forest types have different songs (Goodman et al., 1997). All of these species except *Coracopsis nigra* and *Nectarinia souimanga* are restricted to lower elevation humid forest (<1500 m). *Neomixis tenella* and *N. striatigula* were both absent from humid forest between 1500 and 1950 m on the eastern side of the RNI d'Andohahela, but they were present in transitional forest at about 1500 m on the western slope of the massif. *Coracopsis nigra* and *Nectarinia souimanga* were also present in these transitional forests. For these four species, it is not known which subspecies occur in the transitional forest.

The fact that the nine species listed above occur as separate forms in the two forests suggests that populations of these species in the two habitats are separate and do not experience significant gene interchange. Of the other 17 forest birds that occur in both habitats, at least the four raptors, *Leptosomus discolor*, *Cuculus rochii*, *Zoonavena grandidieri*, and *Hypsipetes madagascariensis*, are capable of relatively long-distance movement

and so might be expected to show dispersal across the mountain chain. Thus, only eight forest bird species (9% of the total), *Streptopelia picturata*, *Centropus toulou*, *Newtonia brunneicauda*, *Terpsiphone mutata*, *Nectarinia notata*, *Zosterops maderaspatana*, *Dicrurus forficatus*, and *Foudia madagascariensis*, appear to be phenotypically identical in both forest types.

Methodological Considerations

In parcel 1 of the RNI d'Andohahela, species richness only starts to drop off at about 1,200 m (Fig. 12-2). Correction for surface area (as suggested by Rahbek, 1995) or controlling for sampling effort by using the number of days of sampling associated with measures of species richness inflates species richness unrealistically in sites with few samples. The reason for this seems to be that most point count stations within an elevational zone generally contained the same species. Point count sites at species-rich elevations simply hold more species than those at species-poor elevations; increasing the point count sample size beyond 12 or 15 does not increase the number of species recorded at an elevational sample. One should thus evaluate the variation in species richness as a function of elevation for humid forest birds in Madagascar without correcting for surface area sampled or controlling for overall sampling effort. The only form of controlling for sampling effort should be the use of a similar sampling effort (whether surface area, point counts, or days) at each site. It appears that a relatively smaller proportion of the total species is recorded on point counts at lower elevations (Table 12-1), so the number of days spent sampling (including sampling by active searching) would probably be a more appropriate measure to keep constant were a comparison between different elevational zones required.

Species Densities

Species densities are broadly comparable to those calculated in the Réserve Spéciale (RS) d'Anjanaharibe-Sud (Hawkins et al., 1998), and the RNI de Zahamena (Hawkins et al., in press). For instance, the calculated density of *Atelornis crossleyi* in the higher altitude forest varied from 43 to about 66 singing individuals per km² in the RS d'Anjanaharibe-Sud, 98 individuals per km² in

the RNI de Zahamena, and 67 individuals per km² in parcel 1 of the RNI d'Andohahela (Table 12-3). *Cryptosylvicola randrianasoloi* occurred at between 21 and 135 individuals per km² in the RS d'Anjanaharibe-Sud, compared to about 119 individuals km² in the present study (Table 12-3). The density of *Phyllastrephus madagascariensis* was higher in parcel 1 of the RNI d'Andohahela than in other sites; it varied from 67 individuals per km² in the RS d'Anjanaharibe-Sud to 53 per km² in the RNI de Zahamena, and it was between 157 and 214 per km² in the present study. Densities of *Nesillas typica* are often extremely high, especially in montane forests. In the RS d'Anjanaharibe-Sud, about 267 individuals per km² were estimated at 1260 m, rising to 1,807 per km² at 1650 m and 1,547 per km² at 1950 m. At 1500 m in the RNI de Zahamena, a density of about 2,600 individuals per km² was estimated. In the RNI d'Andohahela, estimates ranged from around 790 per km² at 1500 m to 1,265 per km² at 1875 m.

Conservation and Management Implications

With regard to conservation management, the most important ornithological observations recorded during the inventory of the RNI d'Andohahela included the presence of good populations of *Newtonia fanovanae* at 440 m and the occurrence of *Xenopirostris pollenii* at much higher elevations than previously known (Langrand, 1990). In addition, large populations of *Atelornis crossleyi* and *Neodrepanis hypoxantha* were found; these species have been recorded recently in similar montane forests at other sites (Goodman & Putnam, 1996; Hawkins et al., 1998, in press). The presence of five bird species limited to lowland forest (a higher figure than any other elevational zones), coupled with the threat of forest clearance for agriculture within this altitudinal range across Madagascar (Green & Sussman, 1990), means that in the RNI d'Andohahela, as in other eastern humid forests, the lowland sector should be given high priority for immediate conservation activity.

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Chapter 13

Lipotyphla (Tenrecidae and Soricidae) of the Réserve Naturelle Intégrale d'Andohahela, Madagascar

Steven M. Goodman,¹ Paulina D. Jenkins,² and Mark Pidgeon³

Abstract

Lipotyphla (Soricidae and Tenrecidae) were studied in extreme southeastern Madagascar in two different parcels of the Réserve Naturelle Intégrale d'Andohahela: on the eastern slopes of humid forest (parcel 1) in five elevational zones between 440 and 1875 m, and in the spiny bush (parcel 2) with a single site at 120 m. Thirteen species of lipotyphlans were recorded in parcel 1, including 10 species of *Microgale*, whereas only three species of lipotyphlans, and no *Microgale*, were documented in parcel 2. Although these two parcels are separated by a distance of only 20 km, no species of lipotyphlan was found to occur in both parcels.

Within parcel 1 three species of Tenrecidae occurred across the complete elevational range: *Microgale longicaudata*, *M. parvula*, and *M. dobsoni*. The only species restricted to a single elevational zone was *Oryzorictes hova*, which was recorded at 1875 m. The greatest species richness of Tenrecidae was nine (including eight species of *Microgale*), at 1200 m; the other elevational zones had eight species of Tenrecidae, of which six to eight were members of the genus *Microgale*. Densities of lipotyphlans in the 1875 m zone were exceptionally high, with up to 77.9% capture rates in the pitfall lines. Evidence was found for two distinct communities within the humid forest (parcel 1): a lowland to mid-montane (440–1200 m) fauna consisting of *Microgale principula*, *M. thomasi*, and *Tenrec ecaudatus*, and a montane to sclerophyllous forest fauna that included *M. gracilis*, *M. gymnorhyncha*, and *Oryzorictes hova*. *Microgale fotsifotsy*, *M. cowani*, and *M. soricoides* had elevational distributions that crossed over these two habitat communities. New information is presented here on morphology, reproduction, development, ecology, and systematics, including a partial taxonomic revision of the genus *Oryzorictes*.

The three species of lipotyphlans recorded in parcel 2, *Geogale aurita*, *Echinops telfairi*, and *Suncus madagascariensis*, have distributions across much of the arid southern and western portions of the island. When all sources of information are combined, 16 species of Lipotyphla have been recorded within the reserve, and 10 of those belong to the genus *Microgale*.

Résumé

Les études sur les Lipotyphla (Tenrecidae et Soricidae) ont été effectuées dans l'extrême Sud-Est de Madagascar dans deux Parcelles différentes de la Réserve Naturelle Intégrale d'Andohahela: sur les versants Est de la forêt humide (Parcelle 1) étalés sur cinq zones d'altitudes comprises entre 440 m et 1875 m, et dans une zone de broussailles épineuses

¹ Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, IL 60605-2496, U.S.A.

² The Natural History Museum, Cromwell Road, London SW7 5BD, United Kingdom.

³ Route de St. Cergue, 1270 Trélex, Switzerland.

(Parcelle 2) comprenant un seul site à 120 m d'altitude. Treize espèces d'insectivores sont inventoriées à l'intérieur de la Parcelle 1, y compris 10 espèces de *Microgale*, contre seulement trois espèces d'insectivores et aucun *Microgale* enregistré dans la Parcelle 2. Bien que ces deux Parcelles soient à une distance de 20 km seulement l'une de l'autre, aucune espèce commune d'insectivore a été décelée dans les deux Parcelles.

A l'intérieur de la Parcelle 1, trois espèces de Tenrecidae apparaissent à travers l'ensemble des zones d'altitudes différentes: *Microgale longicaudata*, *M. parvula*, et *M. dobsoni*. La seule espèce limitée à une zone d'altitude unique est l'*Oryzorictes hova*, inventoriée à une altitude de 1875 m. La communauté la plus importante de Tenrecidae est composée de 9 espèces (comprenant 8 espèces de *Microgale*) se trouvant à une altitude de 1200 m; au niveau des autres zones d'altitudes différentes, on rencontre 8 espèces de Tenrecidae dont 6 à 8 espèces appartiennent au genre *Microgale*. Les densités d'insectivores dans la zone d'altitude 1875 m sont exceptionnellement élevées, avec une proportion de capture s'élevant jusqu'à 77.9% au niveau des pièges. Une découverte a été faite sur deux communautés distinctes à l'intérieur de la forêt humide (Parcelle 1): une faune typique des zones variant d'une altitude basse à une altitude à mi-flanc d'une montagne (de 440 m à 1200 m) composée de *Microgale principula*, *M. thomasi*, et *Tenrec ecaudatus*, et une faune typique des zones de montagnes à des zones de forêts sclerophyles comprenant *M. gracilis*, *M. gymnorhyncha*, et *Oryzorictes hova*. Plusieurs espèces sont réparties selon les altitudes dont le cas des habitats de ces deux populations: *M. fotsifotsy*, *M. cowani*, et *M. soricoides*.

De nouvelles informations sont présentées sur la morphologie, la reproduction, le développement, l'écologie et les systématiques, comprenant une révision partielle taxonomique du genre *Oryzorictes*.

Les trois espèces d'insectivores inventoriées dans la Parcelle 2 possèdent des colonies à travers la plupart des parties arides du Sud et de l'Ouest de l'île. Ces espèces comprennent: *Geogale aurita*, *Echinops telfairi*, et *Suncus madagascariensis*. En considérant toutes les sources d'information, 16 espèces de Lipotyphla ont été inventoriées à l'intérieur de la réserve, dont 10 appartiennent au genre *Microgale*.

Introduction

The southeastern corner of Madagascar contains a remarkable range of landscapes, from humid forest to some of the driest areas on the island. Reflected in this array of biotopes are varying natural habitats that are often separated by abrupt ecotones. The Réserve Naturelle Intégrale (RNI) d'Andohahela contains most of these ecological zones. It is divided into three parcels (see Chapter 1). Parcel 1 is a large block of humid forest (63,100 ha) at the southern end of the north-south-aligned Anosyenne Mountain chain that ranges in altitude from about 300 to slightly less than 2000 m. Local rainfall ranges from 1,500 to at least 2,000 mm annually. Within parcel 1 is a wide range of forest types, including areas classified as High Mountain Domain (one of the phytogeographic zones recognized by Humbert [1955]). Parcel 1 is of particular biogeographical interest because it contains physically diverse areas with correspondingly distinct flora and fauna. To the west of the Anosyennes and within the rain shadow of the mountain range is parcel 2, a large-

ly intact block (12,400 ha) of semiarid spiny bush and gallery forest ranging in altitude from 110 to 1005 m (Nicoll & Langrand, 1989; Goodman et al., 1997). The yearly rainfall in this area is on the order of 600–700 mm, with a pronounced dry season of 5–6 months. The ecotone between parcels 1 and 2 is dramatic and abrupt: in just a few kilometers there is a shift from humid to dry forest. At the very southern end and on the west-facing slopes of the Anosyenne Mountain Range is parcel 3 of the RNI d'Andohahela. This parcel contains a small area (500 ha) of transitional habitat with elements of both dry and wet forest.

The Lipotyphla (the order currently recognized as including the families Erinaceidae, Solenodontidae, Chrysochloridae, Tenrecidae, Soricidae, Talpidae, and their fossil relatives, all of which were formerly placed in the Order Insectivora; see Butler, 1988) is represented in Madagascar by the Tenrecidae and Soricidae. Previous work on the lipotyphlan fauna of the region includes a 1989–1990 study of the small mammal fauna of southeastern Madagascar conducted by G. Ken Creighton, D. Rakotondravony, and colleagues. This

study was part of an environmental impact study associated with the QIT-FER mining project; nothing has yet been published on this material. Creighton et al. visited a wide variety of sites and habitats in the region. Material collected during this study is deposited in the Département de Biologie Animale, Université d'Antananarivo (UA) and the National Museum of Natural History (USNM), Washington, D.C. O'Connor et al. (1987) and Nicoll and Langrand (1989) discuss lipotyphlans from the reserve; in most cases their records are based on direct observations or information from people living near or regularly passing through the reserve.

During a small mammal survey undertaken by two of us (S.M.G. and M.P.) in 1995, a transect was conducted up the eastern side of parcel 1 of the reserve and five elevational zones were sampled (440, 810, 1200, 1500, and 1875 m). A sixth site was sampled in the spiny bush of parcel 2. Not surprisingly, considerable differences were evident between the small mammal faunas of these two parcels, and altitudinal variation was demonstrated within the fauna of parcel 1.

The purpose of this chapter is to provide information on the distribution, ecology, and species richness of lipotyphlans of this region, document their elevational distribution within the humid forests of parcel 1, and summarize the remarkable level of species turnover between parcel 1 and 2. The humid forests of parcel 1 represent the southern limit of this habitat on Madagascar, and thus the distributional data from the site help to define the geographical ranges of the locally occurring small mammals.

The Lipotyphla occurring in Madagascar include four subfamilies of the family Tenrecidae (three of which are endemic) and two species of *Suncus* belonging to the family Soricidae. Three of the four families of Tenrecidae (Tenrecinae, Oryzorictinae, and Geogalinae) are represented in the RNI d'Andohahela, as is one soricid, *Suncus madagascariensis* (Coquerel, 1848). Information on external and craniodental morphology, measurements, variation, population structure, and reproduction is given under Systematics, below. Morphological data are presented as brief key features for species that have been recorded in previous reports (Jenkins et al., 1996, 1997; Goodman & Jenkins, 1998). More complete data are provided for those taxa not so recorded, namely *Echinops telfairi* Martin, 1838, *Oryzorictes hova* A. Grandidier, *Geogale aurita* Milne Edwards & A. Grandidier, 1872, and *S. madagascariensis*.

Detailed descriptions of these species were previously sparse or lacking. The chapter also includes a partial revision of the genus *Oryzorictes*.

Materials and Methods

Trap Lines

Pitfall traps with associated drift fences were the principal means of capturing lipotyphlans. In all of the elevational zones visited within humid forest (440, 810, 1200, 1500, and 1875 m), as well as the spiny bush site (120 m), three separate pitfall lines (generally one in a valley bottom, one on a slope, and one on a ridge crest) were installed. Each line was 100 m long and consisted of 11 buckets, 10 m apart, in operation for a minimum of 6 nights. More details on the technique are given in Chapter 11. A few Lipotyphla were also captured with standard Sherman live traps. The trap types, placement, baits, etc. for these lines are described in Chapter 14.

Traps and pitfalls were visited at least twice per day, once at dawn and again in the late afternoon. A "trap-day" and "bucket-day" are defined as a 24-hr period (dawn to dawn) of use for one of these devices. After rains the buckets were sponged dry. The inventory of the RNI d'Andohahela was conducted between 19 October and 15 December 1995, a seasonal period when all Tenrecidae, including those that hibernate or aestivate, are expected to be active (Stephenson, 1994a).

Captured animals were either released or prepared as standard museum skins with associated skulls and skeletons, as fluid preserved carcasses, or as full skeletons. Voucher specimens are deposited in the Field Museum of Natural History (FMNH), Chicago, and a representative series was returned to UA. Specimens deposited in the latter institution immediately after the survey have not yet been catalogued and are individually referenced by the collector's field numbers (UA-SMG or UA-MP).

Measurements

Cranial measurements were taken using digital calipers to within 0.1 mm or using a microscope measuring stage; external measurements were made using a standard rule to within 1 mm. The dental nomenclature follows that of Mills (1966), Swindler (1976), Butler and Greenwood (1979),

and MacPhee (1987). Dental notations are given in parentheses in the text. Premaxillary and maxillary teeth are denoted by uppercase letters and mandibular teeth by lowercase letters, as follows: incisor (I/i), canine (C/c), premolar (P/p), molar (M/m). The prefix 'd' indicates deciduous teeth; thus (dl3) refers to the deciduous third upper incisor. The following measurements were made of specimens in the flesh or from prepared crania. Abbreviations and definitions for these measurements (all in millimeters, with the exception of weight [WT], in grams) follow.

BB (breadth of braincase): greatest distance measured across the squamosals

BL (braincase length): from the superior articular facet of the occipital condyle, parallel to the long axis of the skull

CIL (condyloincisive length): cranial length from anteriormost portion of first upper incisor to occipital condyle

Ear (ear length): measured from the notch at the base of the ear to the distalmost edge of the pinna

HB (head-and body length): measured from the tip of the nose to the distalmost point of the body (at base of tail)

HF (hind foot length): measured from the back edge of the heel to the tip of the longest toe (not including claw)

IOB (interorbital breadth): shortest distance across the frontals between the orbital fossae

LMR (maxillary toothrow length): distance of the occlusal surface from first incisor to last molar

ML (mandible length): measured from the condylar process across the length of the mandible to the alveolus of first incisor

NL (nasal length): greatest length of nasal bone

TL (tail length): measured from the base of the tail (at right angles to the body) to the end of the distalmost vertebra; does not include terminal hair tufts

UTL (upper toothrow length): from anterior of first upper incisor to posterior of third upper molar, parallel to the long axis of the skull

WT (weight): measured in grams (g) with Pesola spring scales. Animals weighing <10 g were weighed to within 0.2 g; those weighing between 10 and 100 g were weighed to within 0.5 g

ZB (zygomatic breadth): greatest breadth across the zygomatic processes

Reproductive condition was recorded for males as length \times width of the testes and degree of convolution of the epididymis. Females were noted

as nonperforate or perforate, nonparous or parous, and the number and location of any embryos and placental scars were recorded. The mammary formula is presented as the number of paired axillary, abdominal, or inguinal mammae.

The following age classes are recognized: "Infant" refers to individuals in which the deciduous antemolar dentition and the molars are not fully erupted; premaxillary, parietal, and basioccipital sutures are unfused. "Juvenile" includes individuals in which the molars are fully erupted, the deciduous antemolar dentition is erupted and in the process of replacement by the permanent teeth and cranial sutures are in the process of fusing. The eruption sequence of the permanent teeth was subdivided into four stages by MacPhee (1987); these stages have been accepted in this text unless otherwise stated. "Adult" individuals have a fully erupted permanent dentition and the cranial sutures are generally fused, although their position is more or less clearly marked.

Other Abbreviations

Besides the sites designated RNI (Réserve Naturelle Intégrale), there are two other designations for protected sites in Madagascar: PN (Parc National) and RS (Réserve Spéciale).

BM (NH) The Natural History Museum, London (formerly British Museum [Natural History])

FMNH Field Museum of Natural History, Chicago

MCZ Museum of Comparative Zoology, Harvard

MNHN Muséum National d'Histoire Naturelle, Paris

MP Field catalog of Mark Pidgeon

SMG Field catalog of S. M. Goodman

UA Département de Biologie Animale, Université d'Antananarivo, Antananarivo

UMMZ University of Michigan Museum of Zoology, Ann Arbor.

Systematics

Family Tenrecidae

Subfamily Tenrecinae

Echinops telfairi Martin, 1838

HOLOTYPE—BM (NH) 1855.12.24.86: skin, skull, and skeleton collected by William Telfair.

TABLE 13-1. External measurements (mm) and weight (g) of Malagasy Lipotyphla recorded in the RNI d'Andohahela, excluding *Microgale*.

Species	HB*	TL	HF	Ear	WT
<i>Oryzorictes hova</i>	107.14 ± 4.30 101–112 (7)	52.86 ± 1.86 51–55 (7)	17.71 ± 0.95 16–19 (7)	12.00 ± 0.82 11–13 (7)	34.00 ± 3.71 28–40 (7)
<i>Echinops telfairi</i>	— 13	13	20	25	—
<i>Suncus madagascariensis</i>	44.71 ± 3.77 39–51 (7)	33.00 ± 1.73 31–35 (7)	7.86 ± 0.69 7–9 (7)	6.57 ± 0.53 6–7 (7)	2.46 ± 0.53 1.8–3.2
<i>Geogale aurita</i>	67.80 ± 5.00 61–76 (6)	38.67 ± 2.42 34–41 (6)	11.67 ± 0.52 11–12 (6)	17.00 ± 1.55 15–18 (6)	7.03 ± 1.34 5.5–8.5 (6)

The mean, standard deviation, and range are given, with sample size in parentheses.
* HB = head and body length; TL = total length; HF = hind foot length; Ear = ear length; and WT = weight.
See text (p. 190) for further explanation of abbreviations.

TYPE LOCALITY—Madagascar(?).
REFERRED MATERIAL—FMNH 156489: 7.5 km ENE of Hazofotsy, 24°49'S, 46°36'E, 120 m.
KEY FEATURES—Dorsum covered with spines; external tail absent. Dorsal profile of skull only slightly curved; rostrum short, deep, and broad; interorbital region elongated, frontals not inflated; braincase deeper than interorbital region; braincase short, lambdoid crest well developed. Dental formula 2/2 1/1 3/3 2/2 = 32; I1 taller than C; no diastemata.
MEASUREMENTS—External measurements are presented in Table 13-1.

REMARKS—This specimen was collected in slightly disturbed spiny forest. *Echinops* is an animal of dry habitat, and the record from parcel 2 of the RNI d'Andohahela is apparently the easternmost occurrence of this species in southern Madagascar. On the basis of discussions with forest guards and local people living near the reserve, this species has been reported to occur in parcel 1; we strongly suspect that records of hedgehog-like spiny tenrecids from this area are of *Setifer* and not *Echinops*. *Echinops telfairi* is known to live in a variety of ecotypes from spiny bush to dry deciduous forest, and it seems somewhat resilient to selective logging (Nicoll & Langrand, 1989; Goodman & Ganzhorn, 1994; Ganzhorn et al., 1996).

Setifer setosus (Schreber, 1777)

HOLOTYPE—Unknown.
TYPE LOCALITY—Unknown.
REFERRED MATERIAL—FMNH 156490: 8 km NW of Eminiminy, 24°37'S, 46°45'E, 440 m.
KEY FEATURES—Dorsum covered with spines; very short spinous tail present. Skull moderately

robust, dorsal profile curved in lateral view; rostrum deep and broad; interorbital region broad and elongated, frontals posterodorsally inflated; interorbital region deeper than braincase; braincase short, lambdoid crest present. Dental formula 2/2 1/1 3/3 3/3 = 36; I1 well developed, slightly shorter than C; short diastemata on either side of C and first lower premolar (p2).
REMARKS—The single specimen was found in undisturbed lowland forest with relatively open understory. It has been previously reported to occur in parcel 1 and inferred to occur in parcel 3 on the basis of published maps of its distribution (O'Connor et al., 1987). This species is broadly distributed across the eastern humid forests, generally at lower-lying elevations, from the RNI d'Andohahela north to the PN de la Montagne d'Ambre in the Antsiranana region (Raxworthy & Nussbaum, 1994; Goodman et al., 1996a). It is also known from a variety of sites in western deciduous forest (Ganzhorn et al., 1996) and spiny forest (Nicoll & Langrand, 1989).

Tenrec ecaudatus (Schreber, 1777)

HOLOTYPE—Unknown.
TYPE LOCALITY—Unknown.
REFERRED MATERIAL—FMNH 156491: 12.5 km NW of Eminiminy, 24°35'S, 46°44'E, 810 m; FMNH 156492, UA-SMG 7547: 13.5 km NW of Eminiminy, 24°35'S, 46°44'E, 1200 m.
KEY FEATURES—The largest of the Tenrecinae. Dorsal pelage of coarse bristly hair intermixed with spines; short tail present. Skull elongated; rostrum with deep sockets in ventrolateral region of the premaxillae, which accommodate the lower canines when the jaw is closed; interorbital region narrow, elongated; braincase short, narrow, an-

gular, pronounced sagittal and lambdoid crests form deep posterodorsal flanges. Dental formula $2/3 \ 1/1 \ 3/3 \ 3/3 = 38$; upper and lower canines very long, robust, and prominent; pronounced diastemata on either side of C and posterior to c; short diastemata posterior to first upper and lower premolars.

REMARKS—Specimens were collected in undisturbed lowland and primary montane forest. *Tenrec ecaudatus* has been previously reported in parcel 1 of the reserve and thought to occur in parcel 2 on the basis of published distributional maps (O'Connor et al., 1987). This species is broadly distributed across Madagascar and occurs in a wide variety of habitats, including humid and deciduous forests as well as spiny bush. It seems to thrive in disturbed areas, even in the presence of human hunting pressure and forest exploitation (Ganzhorn et al., 1990, 1996; Raharivololona, 1996).

Subfamily Geogalinae

Geogale aurita Milne Edwards & A. Grandidier, 1872

HOLOTYPE—MNHN no. 267: unsexed specimen in alcohol, skull extracted, collection date unknown (Rode, 1942).

TYPE LOCALITY—"Morondova (= Morondava) et Tullear" (= Toliara).

REFERRED MATERIAL—FMNH 156350–156352, 156551–156553: 7.5 km ENE of Hazofotsy, 24°49'S, 46°36'E, 120 m.

KEY FEATURES—Small, shrew-like, similar in overall appearance to *Microgale* but pinnae large and prominent, tail covered with fine hairs, HF short relative to HB (see Table 13-1 for dimensions). Pelage soft, very short, and not dense. Dorsal fur coloration varies from light gray to a light reddish brown, ventrum buffy white. Cranium elongated, dorsal profile straight, inclining gradually from rostrum to occiput; rostrum narrow; zygomatic plate broad, with prominent anterior margin; interorbital region narrow and elongated; braincase short, angular, lambdoid crest pronounced. Dental formula $2/2 \ 1/1 \ 3/2 \ 3/3 = 34$; I1 large, slightly proodont, distostyle well developed, small diastema present between first and second upper incisors; second incisor and C small, similar in height to distostyle of I1; P2 and P3 very small, less than distostyle of C in height; talons of P4, M1, and M2 anteroposteriorly com-

pressed; M3 highly compressed anteroposteriorly, buccolingually elongated; i1 moderately large, slightly procumbent, second lower incisor slightly shorter than posterior cuspid of i1; c reduced in size; first lower premolar very small, second lower premolar with well-developed protoconid; talonoid of m3 reduced to a single cuspid.

MEASUREMENTS—External measurements are presented in Table 13-1.

POPULATION STRUCTURE AND REPRODUCTION—The testes of one male with convoluted epididymides (FMNH 156351) measured 8×5 mm. One pregnant female (FMNH 156552) contained two embryos in the left and three in the right oviduct that measured 3 mm in crown to rump length. Litters of up to five individuals have been reported in this species (Stephenson, 1993). Mammary formula: 1-1-2 ($n = 1$), 2-0-2 ($n = 1$).

REMARKS—All specimens were collected in slightly disturbed spiny forest. This species is known to occur in a variety of dry forest types in southern and western Madagascar. The occurrence of *Geogale* in parcel 2 of the RNI d'Andohahela represents the eastern known limit of this species in southeastern Madagascar. It has been recorded in spiny bush, deciduous forest, and transitional habitats between these two forest types (Nicoll & Langrand, 1989; Goodman & Ganzhorn, 1994; Ganzhorn et al., 1996; Goodman & Rasoloarison, 1997).

Subfamily Oryzorictinae

Oryzorictes hova A. Grandidier, 1870

Oryzorictes talpoides G. Grandidier and Petit, 1930

HOLOTYPE—MNHN type no. 262, CG 1887-874: adult female in alcohol, skull extracted, collection date unknown.

TYPE LOCALITY—"Ankaye (= Ankay, along the Mangoro River near Lac Alaotra) et Antsianak" (= Antsianaka, region to the east of Lac Alaotra; Viette, 1991).

REFERRED MATERIAL—FMNH 156485–156488, 156601–156603: 20 km SE of Andranandambo, 24°33'S, 46°43'E, 1875 m.

KEY FEATURES—Pelage soft, slightly iridescent; TL approximately half HB (TL:HB mean 49.51 ± 2.70 , range 46.0–53.9, $n = 5$); forefeet with very enlarged claws; broad naked rhinarium; eyes very small; ears small, concealed in pelage. Skull moderately robust, premaxillae dorsolaterally

flared, braincase short, broad and deep, lambdoid crests well marked; I3 very small, approximately as tall as distostyle of I2; diastema present between I3 and C, forming a sulcus to accommodate the distal tip of c; upper and lower canines markedly taller than all other teeth; distostyle of C very small.

MEASUREMENTS—External measurements are presented in Table 13-1.

POPULATION STRUCTURE AND REPRODUCTION—The sex ratio of females to males was 1:2. No juveniles were present in the sample collected. The testes of one male (FMNH 156601) with convoluted epididymides measured 6×5 mm. One female (FMNH 156602) was pregnant, carrying one embryo in the left and two in the right oviduct that measured 5 mm in crown to rump length. Another female (FMNH 156603) with permanent dentition was imperforate.

REMARKS—All specimens collected during the 1995 survey were taken in transitional primary forest between upper montane and sclerophyllous forest, either in valley bottoms or on ridge crests. The only exception is the remains of an *Oryzorictes hova* that were recovered from the digestive system of a *Pseudoxyrhopus* snake captured at the 1200 m site. Other records from southeastern Madagascar include one animal taken at about 50 m at Bezavona near the base of Pic St. Louis, 1 km west of Tolagnaro (USNM 577052) and two at 750 m in the Marosohy Forest, along the northeastern border of parcel 1 of the RNI d'Andohahela (USNM 578789, 578913). This species has a broad distribution across the humid portions of the island and is known to occur in lowland marsh and rice paddy habitats up to high-elevation montane and sclerophyllous forest.

TAXONOMIC COMMENTS—In 1870 A. Grandidier described a new genus and species of lipotyphlan from the northern portion of eastern Madagascar as *Oryzorictes hova*. He characterized the genus as having a long rhinarium terminating in small nostrils; very small eyes; medium-sized round ears; forefeet with four digits, three with large and strongly recurved claws; hind feet with five digits; and a dental formula of $3/3 \ 1/1 \ 6/6$ (premolars and molars combined).

As pointed out by G. Grandidier and Petit (1930), the holotype of *Oryzorictes hova* possesses a highly reduced fifth digit on the forelimbs, not just four digits as stated by A. Grandidier (1870). This mistake was reiterated by several authors (e.g., Dobson, 1882). Subsequent to the publication of the *O. hova* description, a second spe-

cies in this genus, *O. talpoides*, with five digits on the forefoot, was named by G. Grandidier and Petit (1930). The type locality of *O. talpoides* is near Marovoay in northwestern Madagascar, not far from Mahajanga. A third member of this genus, *O. tetradactylus*, was named by Milne Edwards and A. Grandidier in 1882; this species has four digits on the forelimbs.

A further discrepancy between the characters noted in the description of *Oryzorictes hova* and the actual type specimen has to do with the dental formula. Although A. Grandidier (1870) clearly stated that the type specimen had an I3, there is no evidence of this tooth, its root, or any erupting structure. This difference in incisor count was not noted by G. Grandidier and Petit (1930) or Dobson (1882) in their descriptions of *O. talpoides*, but it was used as one of the distinguishing characters by Genest and Petter (1975) to differentiate *O. hova* and *O. talpoides*. The latter authors noted that *O. hova* lacked an I3. On the basis of tooth eruption and suture ossification, the holotype of *O. hova* represents an adult individual.

After examination and measurement of the holotypes of *Oryzorictes hova* and *O. talpoides* (MNHN 264) and nearly 30 specimens of five-toed *Oryzorictes* collected from a variety of localities on Madagascar, no individual other than the holotype of *O. hova* has been found lacking the I3. Furthermore, cranial measurements of the holotypes of *O. hova*, *O. talpoides*, and five-toed *Oryzorictes* show broad overlap, and these species cannot be differentiated based on these characters (Table 13-2).

Another character that has been proposed to differentiate *Oryzorictes hova* and *O. talpoides* is the size of the pollex (Grandidier & Petit, 1930; Genest & Petter, 1975). This character is difficult to measure in dried specimens, and it is impossible to compare such measurements with specimens preserved in fluid. On the basis of the collection from Andohahela and material housed in BM(NH) that was collected from a variety of localities in the eastern humid forest, however, there is considerable variation in this character at the population level as well as the regional level. Therefore we conclude that it is of no use in differentiating among types of five-toed *Oryzorictes*.

Each of the specimens we have examined in museum collections that was previously determined as *Oryzorictes hova* possesses an I3 (e.g., FMNH 5641; BMNH 94.290, 97.9.1.77) and on the basis of the Genest and Petter (1975) key is referable to *O. talpoides*. Furthermore, there are

TABLE 13-2. Selected cranial measurements (mm) of the holotypes of *Oryzorictes hova* and *O. talpoides*, plus specimens of *Oryzorictes* with five digits on the forelimbs.

Species	CIL*	ZB	IOB	BB	UTL	LMR	NL	ML
Holotype of <i>Oryzorictes hova</i> (MNHN type no. 262, CG 1887-874)	29.6	12.3	6.6	13.2	14.5	9.9	14.1	20.8
Holotype of <i>Oryzorictes talpoides</i> (MNHN type no. 264)	30.8	11.5	6.7	13.2	15.1	9.4	13.7	22.6
Specimens of <i>Oryzorictes</i> with five digits on the forelimb	29.5 ± 0.86 28.0-31.6 (n = 20)	11.9 ± 0.60 11.2-13.3 (n = 25)	6.7 ± 0.30 6.4-7.5 (n = 25)	13.3 ± 0.44 12.6-14.0 (n = 15)	14.5 ± 0.52 13.0-15.3 (n = 29)	8.7 ± 0.33 8.1-9.3 (n = 23)	13.8 ± 0.74 12.2-15.2 (n = 20)	21.3 ± 1.00 19.1-22.9 (n = 23)

For multiple measurements, the mean, standard deviation, and range from minimum to maximum are given, with the number of specimens in parentheses. All of the specimens are adult.

*CIL = condyloincisive length; ZB = zygomatic breadth; IOB = interorbital breadth; BB = breadth of braincase; UTL = upper toothrow length; LMR = maxillary toothrow length; NL = nasal length; and ML = mandible length. See text (p. 190) for further explanation of abbreviations.

few published records of *O. hova*. Stephenson (1994b) reported capturing individuals of *O. hova* in the RS d'Analamazaotra (18°28'S, 48°28'E) and in the forest of Anandrivola (15°46'S, 49°36'E), although how the animals were identified was not mentioned explicitly. He further noted that the specimen obtained at Anandrivola was close to a site from which *O. talpoides* had been reported (Heim de Balsac, 1972) and that the two species might be locally sympatric.

On the basis of material available to us we conclude that the various characters proposed to allow one to distinguish between *Oryzorictes hova* and *O. talpoides* show broad overlap and are not useful to differentiate these two taxa. It is odd that the only known specimen of an adult five-toed *Oryzorictes* lacking the I3 is the holotype of *O. hova*, but such dental anomalies have been observed in other members of the Tenrecidae (Dobson, 1882; Leche, 1907; Heim de Balsac, 1972). On the basis of current evidence, we conclude that *O. talpoides* and *O. hova* represent the same species and that the former name is a junior synonym of the latter.

Microgale cowani Thomas, 1882

HOLOTYPE—BM(NH) 82.3.1.25: adult female body in alcohol, skull extracted, collected mid-March to mid-February 1880 by the Reverend W. Deans Cowan.

TYPE LOCALITY—Ankafana Forest, eastern Bet-sileo (Ankafana = Ankafina, Fianarantsoa, Fianarantsoa Province, 21°12'S, 47°12'E; see MacPhee, 1987, Carleton & Schmidt, 1990).

REFERRED MATERIAL—FMNH 156355, 156554, 156555, UA-SMG 7517, 7558: 13.5 km NW of Eminiminy, 24°35'S, 46°44'E, 1200 m; FMNH 156356-156372, 156431, 156556-156563; UAMP 29, 30, UA-SMG 7647: 15 km NW of Eminiminy, 24°34'S, 46°43'E, 1500 m; FMNH 156373-15410, 156564, 156565, UA-SMG 7664, 7665, 7673, 7674, 7685: 20 km SE of Andran-dambo, 24°33'S, 46°43'E, 1875 m.

KEY FEATURES—Medium sized (see Table 13-1); TL moderately short, shorter or subequal to HB. Pelage dark brown dorsally, gray ventrally with a reddish brown wash; tail bicolored, dark brown dorsally, sharply demarcated from paler reddish buff underside. Skull medium in size, rostrum elongated; pronounced diastemata separate teeth of upper anterior dentition from I1 to P3, also on either side of c and p2. All elements of

taloid of m3 present, including hypoconid, entoconid ridge, taloid basin, and entoconid.

MEASUREMENTS—External and cranial measurements are presented in Table 13-3.

POPULATION STRUCTURE AND REPRODUCTION—The sex ratio of females to males was 1:1.3. The ratio of juveniles to adults was 1:1.2. The upper and lower last two molars (respectively M2, M3, m2, and m3) were still in the process of erupting in one juvenile specimen, and M3 and m3 were still erupting in three other specimens. The other juveniles showed a complete deciduous dentition, with all molars erupted; the exception was a single specimen in which the deciduous upper and lower third incisors (d13 and di3) had been shed and their permanent replacements (I3 and i3) were erupting. One adult male with convoluted epididymides had testes measuring 8 × 7 mm. One adult female was pregnant with two embryos in the left and one in the right oviduct. Mammary formula: 0-1-2 (n = 4), 0-2-1 (n = 1), 1-0-2 (n = 1).

REMARKS—This species as currently defined (*sensu* Jenkins et al., 1996) has a broad distribution across the eastern humid forest from the RNI d'Andohahela north to at least the RS d'Anjanaharibe-Sud and occurs from lowland forest to summital zones above the tree line at 2450 m (Langrand & Goodman, 1997; Goodman & Jenkins, 1998).

Microgale dobsoni Thomas, 1884
Nesogale dobsoni Thomas, 1918

HOLOTYPE—BM (NH) 84.10.20.1: immature male, in alcohol, skull extracted. Collected February or March 1884 by W. Waters.

TYPE LOCALITY—Nandésen Forest, Central Betileo (Nandihizana, 10 miles S. of Ambositra—manuscript note in Thomas's private copy of original description. Nandihizana, ca. 20 miles [30 km] SSW of Ambositra; see MacPhee, 1987. Estimated as ca. 20°50'S, 47°10'E).

REFERRED MATERIAL—FMNH 156468, 156598: 8 km NW of Eminiminy, 24°37'S, 46°45'E, 440 m; FMNH 156413: 13.5 km NW of Eminiminy, 24°35'S, 46°44'E, 1200 m; FMNH 156414–156417, 156469, 156470, 156567: 15 km NW of Eminiminy, 24°34'S, 46°43'E, 1500 m; FMNH 156418–156421, 156471, 156566, UA-SMG 7666, 7688: 20 km SE of Andranandambo, 24°33'S, 46°43'E, 1875 m.

KEY FEATURES—Large, TL subequal to or longer than HB. Dorsal pelage brown, venter gray

with buff wash. Skull large and robust, sutures fused and obscure; rostrum moderately broad, interorbital region long; braincase angular, superior articular facets very prominent, lambdoid crest well developed; occipital region reduced in size. Diastemata between I1 and I2 and between I3 and C; I1 larger than I2, i2 considerably larger than c; taloid of m3 reduced, hypoconid low, hypoconulid prominent, entoconid ridge and taloid basin poorly defined, entoconid absent.

MEASUREMENTS—External and cranial measurements are presented in Table 13-3.

POPULATION STRUCTURE AND REPRODUCTION—The sex ratio of males to females was 1:7. No juveniles were collected. Two of the females were lactating. Mammary formula: 0-2-1 (n = 1), 1-0-2 (n = 1), 1-1-2 (n = 3), 1-2-1 (n = 1).

REMARKS—The species was trapped along the complete elevational transect between 440 and 1875 m, although no individual was captured in the 810 m zone. Most specimens were trapped on the ground, but one was obtained 2.5 m above ground on a 3-cm-diameter horizontal branch.

Microgale dobsoni is broadly distributed in the eastern humid forest and is known from numerous sites in the geographical zone between the RNI d'Andohahela north to at least the RS d'Anjanaharibe-Sud (MacPhee, 1987; Jenkins et al., 1996; Goodman & Jenkins, 1998). It is a widespread species that appears to be tolerant of habitat disturbance (Goodman et al., 1996b).

Microgale fotsifotsy Jenkins et al., 1997

HOLOTYPE—UMMZ 168468: adult male in alcohol, skull extracted, collected 13 January 1992 by Christopher J. Raxworthy.

TYPE LOCALITY—Camp 2, Antomboka River, Fitsahana, Parc National de la Montagne d'Ambre, Antsiranana Fivondronana, Antsiranana Province, 12°29'S, 49°10'E, 650 m.

REFERRED MATERIAL—FMNH 156568, 156569: 8 km NW of Eminiminy, 24°37'S, 46°45'E, 440 m; FMNH 156424: 13.5 km NW of Eminiminy, 24°35'S, 46°44'E, 1200 m; FMNH 156570: 15 km NW of Eminiminy, 24°34'S, 46°43'E, 1500 m.

KEY FEATURES—Dorsal pelage pale grayish brown, soft in texture, venter with lighter buffy wash; digits of fore- and hind feet and extreme tail tip contrastingly lighter colored; pinnae prominent and conspicuous; fifth digit of hind foot elongated, scarcely shorter than second. Skull with maxillary process of zygoma at right angles

TABLE 13-3. External and cranial measurements (mm) and weight (g) of *Microgale* recorded in the RNI d' Andohahela.

Species	HB	TL	HF	Ear	WT	CIL	UTL	BB
<i>Microgale parvula</i>								
adults	57.00 ± 5.86 50-65 (5)	61.20 ± 2.59 58-65 (5)	9.80 ± 0.84 9-11 (5)	9.00 ± 0.71 8-10 (5)	3.74 ± 0.58 3.2-4.7 (5)	16.48 ± 0.33 16-16.8 (5)	7.38 ± 0.22 7.1-7.6 (5)	6.62 ± 0.15 6.4-6.8 (5)
juveniles	54.8 ± 2.17 52-58 (5)	62.4 ± 2.07 61-66 (5)	10.00 ± 1.00 9-11 (5)	8.1 ± 0.22 8-8.5 (5)	2.6 ± 0.26 2.2-2.8 (5)	16.16 ± 0.35 15.6-16.5 (5)	7.26 ± 0.22 6.9-7.5 (5)	6.54 ± 0.18 6.3-6.7 (5)
<i>M. fotsifotsy</i>								
adults	65.67 ± 1.15 65-67 (3)	81.67 ± 1.53 80-83 (3)	15.00 (3)	16.00 (3)	7.73 ± 1.21 6.8-9.1 (3)	19.53 ± 0.15 19.4-19.7 (3)	9.37 ± 0.12 9.3-9.5 (3)	9.03 ± 0.25 8.8-9.3 (3)
juvenile	61.00 (1)	78.00 (1)	14.00 (1)	15.00 (1)	5.20 (1)	18.90 (1)	9.10 (1)	8.70 (1)
<i>M. longicaudata</i>								
adults	64.75 ± 1.89 62-66 (4)	139.5 ± 10.41 128-151 (4)	16.4 ± 1.14 15-18 (5)	15.8 ± 0.84 15-17 (5)	6.96 ± 0.85 5.7-7.8 (5)	19.52 ± 0.71 18.7-20.3 (5)	9.12 ± 0.41 8.7-9.6 (5)	8.40 ± 0.31 7.9-8.7 (5)
juveniles	60.18 ± 3.94 52-65 (17)	134.39 ± 13.65 109-156 (18)	16.11 ± 1.02 14-18 (18)	14.82 ± 0.73 14-16 (17)	6.18 ± 1.05 4.5-7.5 (17)	19.16 ± 1.06 17.6-20.8 (18)	8.95 ± 0.50 8.1-9.6 (18)	8.38 ± 0.39 7.6-8.9 (18)
<i>M. cowani</i>								
adults	73.90 ± 3.18 66-79 (14)	65.07 ± 2.56 60-69 (14)	16.27 ± 0.70 15-17 (15)	15.71 ± 0.61 15-17 (14)	13.25 ± 1.15 12-15.5 (14)	22.67 ± 0.32 21.9-23.1 (13)	10.91 ± 0.23 10.4-11.3 (15)	10.31 ± 0.13 10.1-10.5 (13)
juveniles	68.20 ± 2.62 65-72 (10)	63.90 ± 4.33 56-71 (10)	16.30 ± 0.82 15-18 (10)	14.80 ± 0.92 14-17 (10)	9.38 ± 1.14 7.9-11.5 (10)	21.97 ± 0.45 21.3-22.6 (10)	10.49 ± 0.20 10.1-10.8 (10)	9.95 ± 0.24 9.7-10.4 (10)
<i>M. principula</i>								
adults	76.6 ± 3.98 70-80 (5)	155.0 ± 6.04 147-164 (5)	18.2 ± 0.84 17-19 (5)	16.8 ± 0.45 16-17 (5)	10.7 ± 1.10 9.5-12.5	22.36 ± 0.31 22.0-22.8 (5)	10.42 ± 0.26 10.1-10.8 (5)	9.2 ± 0.19 8.9-9.4 (5)
juveniles	70.00 ± 4.58 65-74 (3)	153.0 ± 8.62 144-161 (3)	19.00 ± 1.00 18-20 (3)	15.00 (3)	8.3 ± 0.70 7.5-8.8 (3)	21.67 ± 0.15 21.5-21.8 (3)	10.10 ± 0.17 10.0-10.3 (3)	9.03 ± 0.15 8.9-9.2 (3)
<i>M. soricoides</i>								
adults	82.5 ± 4.14 79-89 (8)	96.38 ± 3.34 91-101 (8)	17.88 ± 0.64 17-19 (8)	17.5 ± 0.54 17-18 (8)	18.13 ± 2.64 14-22 (8)	24.33 ± 0.27 23.9-24.6 (8)	11.73 ± 0.26 11.3-12.0 (8)	11.01 ± 0.27 10.6-11.4 (8)
juvenile	75.0 (1)	90.0 (1)	17.0 (1)	16.0 (1)	13.0 (1)	24.2 (1)	11.6 (1)	10.8 (1)
<i>M. gymnorhyncha</i>								
adults	84.00 ± 4.64 79-91 (5)	67.8 ± 2.78 65-71 (5)	15.4 ± 1.52 14-17 (5)	12.00 ± 0.71 11-13 (5)	15.8 ± 2.39 13.5-19.5 (5)	25.72 ± 0.65 25.0-26.5 (5)	13.56 ± 0.29 13.3-14 (5)	10.22 ± 0.15 10.0-10.4 (5)
<i>M. gracilis</i>								
adults	91.50 ± 2.81 88-96 (6)	86.17 ± 2.23 83-88 (6)	19.17 ± 0.98 18-20 (6)	16.33 ± 1.03 15-18 (6)	23.17 ± 1.13 21.5-24 (6)	27.92 ± 0.37 27.5-28.4 (5)	13.78 ± 0.27 13.5-14.2 (6)	10.82 ± 0.23 10.5-11.1 (5)

TABLE 13-3. Continued.

Species	HB	TL	HF	Ear	WT	CIL	UTL	BB
<i>M. thomasi</i>	adults	68.7 ± 4.88 63-80 (10)	18.3 ± 0.95 17-20 (10)	18.7 ± 0.82 17-20 (10)	22.4 ± 1.91 19.5-25 (10)	26.79 ± 0.32 26.3-27.3 (10)	12.98 ± 0.18 12.7-13.2 (10)	10.96 ± 0.26 10.5-11.3 (10)
	juveniles	67.5 ± 1.73 66-70 (4)	18.0 ± 0.82 17-19 (4)	17.75 ± 0.5 17-18 (4)	17.75 ± 2.60 15-21 (4)	25.7 ± 0.67 25.1-26.6 (4)	12.45 ± 0.45 12.1-13.1 (4)	10.93 ± 0.30 10.6-11.3 (4)
	<i>M. dobsoni</i>							
adults	106.72 ± 9.67 95-130 (9)	108.67 ± 5.45 102-120 (9)	23.33 ± 0.87 22-25 (9)	20.56 ± 1.13 18-22 (9)	32.17 ± 4.47 28-39 (9)	31.61 ± 0.75 30.4-32.5 (9)	15.73 ± 0.36 15.2-16.2 (9)	11.63 ± 0.25 11.3-12.1 (9)

The mean, standard deviation, and range are given, with sample size in parentheses. See legends to Tables 13-1 and 13-2 and text (p. 190) for explanation of abbreviations.

to long axis of cranium; braincase broad and short. Third upper and lower incisors small, I3 slightly greater in crown height than distostyle of I2, i3 subequal in height to posterior accessory cusp of i2; i2 greater in breadth than i1; C and c respectively greater in crown height than P3 and p3.

MEASUREMENTS—External and cranial measurements are presented in Table 13-3.

VARIATION—The small samples available suggest that the population from RNI d'Andohahela averages smaller than those from further north in Madagascar.

POPULATION STRUCTURE AND REPRODUCTION—The sex ratio of females to males was 1:2. The ratio of juveniles to adults was 1:3. One male (FMNH 156569) with permanent dentition was reproductively immature, with nonconvoluted epididymides. The adult female had one placental scar in the right oviduct and two in the left. Mammary formula: 0-1-2 (n = 1).

REMARKS—As with so many of the recent findings concerning new taxa of *Microgale* and information on their geographical range, *M. fotsifotsy* has a broad distribution and is known from sites running the complete length of the eastern humid forest, including the RNI d'Andohahela, RNI d'Andringitra, PN de Ranomafana, RS de Zahamena, RS d'Ambatovaky, RNI de Marojejy, RS d'Anjanaharibe-Sud, and PN de la Montagne d'Ambre (Jenkins et al., 1997; Goodman & Jenkins, 1998). Two individuals (USNM 578787, 578887) have also been recorded (Jenkins et al., 1997) from Marosohy Forest, along the northeastern boundary of parcel 1 of the RNI d'Andohahela, between 650 and 700 m. In general this species is captured in low numbers and across an elevational range from lowland to lower montane forest. For example, in the RNI d'Andohahela up to two individuals were trapped within each elevational zone studied between 440 and 1200 m; in the RNI d'Andringitra two individuals were captured in the 1210 m zone; and in the PN de la Montagne d'Ambre *M. fotsifotsy* has been taken between 650 and 1150 m (Jenkins et al., 1997; Goodman et al., 1996a).

Microgale gracilis (Major, 1896)

Oryzoryctes [sic] *gracilis* Major, 1896

Leptogale gracilis Thomas, 1918

HOLOTYPE—BM(NH) 97.9.1.78: adult of undetermined sex, skin and skull. Collected November 1894 by C. I. Forsyth Major.

TYPE LOCALITY—Ambohitombo Forest (Ambohitombo town, 43 km [by road] SE of Ambositra, 10 km into eastern forest; Fianarantsoa, Fianarantsoa; 20°43'S, 47°26'E; see MacPhee, 1987. MacPhee gives the altitude for this locality variously as 1300 m [1987, p. 6] and 1200 m [1987, table 5], but, as pointed out by Carleton & Schmidt, 1990, the altitude recorded for this locality by Major [1897] is 1400–1500 m).

REFERRED MATERIAL—FMNH 156573: 15 km NW of Eminiminy, 24°34'S, 46°43'E, 1500 m; FMNH 156422, 156423, 156425, 156426, 156571: 20 km SE of Andranandambo, 24°33'S, 46°43'E, 1875 m.

KEY FEATURES—Size large, TL shorter than HB. Pelage dark brown dorsally with buff speckling. Muzzle very long; large, naked rhinarium anteriorly reticulated, striae on posterior region incomplete. Eyes very small; ears small, partially concealed by pelage. Forefeet broad, claws enlarged. Skull very elongated and gracile; rostrum slender, markedly attenuated; braincase rounded, moderately broad and long. Dentition reduced; upper incisors subequal in height, incisors and canine very slender; extensive diastemata between all anterior teeth, particularly P2 and P3; talons on molars very reduced, resembling cingula; talonid of m3 slightly reduced, entoconid lacking.

MEASUREMENTS—External and cranial measurements are presented in Table 13-3.

POPULATION STRUCTURE AND REPRODUCTION—The sex ratio of females to males was 1:5 in the small sample available. Only adults were collected. Testes of two males with convoluted epididymides (FMNH 156571 and 156573) measured respectively 10 × 5 mm and 12 × 7 mm.

REMARKS—MacPhee (1987) noted that this species was very rare in collections. In more recent years it has been recorded at a range of sites in the eastern humid forest (arranged from south to north): RNI d'Andohahela; RNI d'Andringitra (Jenkins et al., 1996); PN de Ranomafana (USNM 449179; Nicoll & Rathbun, 1990); and Forêt de Nosiarivo, Ankaratra Massif (Goodman et al., 1996b). The distribution of *Microgale gracilis* is apparently confined to the southern half of the eastern humid forest.

Microgale gymnorhyncha Jenkins et al., 1996

Microgale gracilis (Major): MacPhee, 1987, in part

HOLOTYPE—FMNH 151807: adult female in alcohol, skull extracted, collected 13 December 1993

by Steven M. Goodman and Christopher J. Raxworthy.

TYPE LOCALITY—Thirty-eight km S of Ambalavao, Réserve Naturelle Intégrale d'Andringitra, on ridge E of Volotsangana River, Fianarantsoa Province, 22°11'39"S, 46°58'16"E, 1625 m.

REFERRED MATERIAL—FMNH 156427, 156428, 156572, 156573: 15 km NW of Eminiminy, 24°34'S, 46°43'E, 1500 m; FMNH 156429, 156574: 20 km SE of Andranandambo, 24°33'S, 46°43'E, 1875 m.

KEY FEATURES—Large, TL shorter than HB. Dorsal pelage dark brown, dark gray-brown ventrum. Muzzle very long, forming a proboscis; rhinarium very large with transversely striated naked region. Eyes very small. Ears small, virtually concealed in pelage. Forefeet broad, claws enlarged. Skull long, moderately gracile; rostrum slender and elongated; braincase short and broad. Dentition moderately reduced with long diastemata between all anterior teeth from I1 to P3 and i2 to p3; talonid of m3 slightly reduced; talonid basin, hypoconid, hypoconulid, and entoconid ridge present, entoconid indicated.

MEASUREMENTS—External and cranial measurements are presented in Table 13-3.

POPULATION STRUCTURE AND REPRODUCTION—The sex ratio of females to males was 1:4 in the small sample available. Only adults were collected, but one of these (FMNH 156574, a male with permanent dentition) was not in reproductive condition and possessed nonconvoluted epididymides. The testes of another male (FMNH 156572) with convoluted epididymides measured 6 × 4 mm. Mammary formula: 1-1-2 (n = 1).

REMARKS—This recently described species is known from a variety of localities in the eastern humid forest (south to north): RNI d'Andohahela, RNI d'Andringitra (Jenkins et al., 1996), PN de Ranomafana (UA), near Fanovana (Jenkins et al., 1996), Forêt d'Andranomay, Anjozorobe (Goodman et al., 1998), and the RS d'Anjanaharibe-Sud (Goodman & Jenkins, 1998). It occurs in montane to sclerophyllous forest and is unknown from lowland humid forest.

Microgale longicaudata Thomas, 1882

Microgale majori Thomas, 1918: MacPhee, 1987

HOLOTYPE—BM(NH) 82.3.1.15: adult female, body in alcohol, skull extracted, collected mid-

February 1879 to mid-March 1880 by the Reverend W. Deans Cowan.

TYPE LOCALITY—Ankafana Forest, eastern Bet-sileo (Ankafana = Ankafina, Fianarantsoa, Fianarantsoa Province, 21°12'S, 47°12'E; see MacPhee, 1987, Carleton & Schmidt, 1990).

REFERRED MATERIAL—FMNH 156576: 8 km NW of Eminiminy, 24°37'S, 46°45'E, 440 m; FMNH 156449, 156450, 156579–156581: 12.5 km NW of Eminiminy, 24°35'S, 46°44'E, 810 m; FMNH 156583, UA-SMG 7542, 7548: 13.5 km NW of Eminiminy, 24°35'S, 46°44'E, 1200 m; FMNH 156430–156433, 156455, 156584: 15 km NW of Eminiminy, 24°34'S, 46°43'E, 1500 m; FMNH 156434–156448, 156451, 156452, 156578, 156593, UA-SMG 7680, 7720–7724, UA-MP 36: 20 km SE of Andranandambo, 24°33'S, 46°43'E, 1875 m.

KEY FEATURES—Small in size, TL very long, more than twice as long as HB; distal portion of tail naked and transversely wrinkled on dorsal surface; fifth hind digit elongated, subequal in length to second digit. Dorsal pelage reddish brown, venter gray with bright reddish buff or buff wash. Skull small, rostrum moderately short; braincase moderately narrow and long. Diastemata present between I1 and I2, on either side of C and P2; well-developed anterior and posterior accessory cusps present on I2, C, and P2; C subequal to or taller than I1; P4 scarcely greater in crown height than P3; p2 caniniform; talonid of m3 with low hypoconid, hypoconulid well developed, narrow talonid basin, reduced entoconid ridge, and entoconid absent.

MEASUREMENTS—External and cranial measurements are presented in Table 13-3.

POPULATION STRUCTURE AND REPRODUCTION—The sex ratio of males to females was 1:1.3. The ratio of adults to juveniles was 1:3.6. The third molars were not fully erupted in two juvenile specimens. All juveniles had completely deciduous anterior dentitions, except for two in which the di3s were in the process of replacement by the permanent teeth. One male with a deciduous dentition (FMNH 156576) was reproductively mature with convoluted epididymides and testes measuring 4 × 3 mm. Mammary formula: 1-0-2 (n = 1), 1-1-2 (n = 1), 1-2-2 (n = 1).

REMARKS—This species is broadly distributed in the eastern humid forests from the RNI d'Andohahela north to the PN de la Montagne d'Ambre (MacPhee, 1987; Jenkins, 1993; Raxworthy & Nussbaum, 1994; Jenkins et al., 1996). An individual tentatively assigned to the *Micro-*

gale longicaudata species group has been reported from the dry deciduous forest near Morondava (Ade, 1996).

Throughout much of its range, this species is sympatric with another long-tailed species, *Microgale principula*. These two species have remarkable modification of the tail for prehensile activity, and they may occupy some aspects of the same arboreal niche (Eisenberg & Gould, 1970; Goodman & Jenkins, 1998). In the RS d'Anjanaharibe-Sud these two species replace one another along an elevational gradient, with *M. principula* occurring in lower-lying forest and *M. longicaudata* on the upper slopes (Goodman & Jenkins, 1998). Although there is a tendency for the same pattern to occur in the humid forest of the RNI d'Andohahela, the two species overlap broadly in elevation between 440 and 1200 m. On the basis of capture results, *M. principula* was more common in the 440 m zone, whereas *M. longicaudata* was more common at higher elevations (Tables 13-4 and 13-5). Both species have also been recorded from PN de Mantady (Jenkins, 1993).

Microgale parvula G. Grandidier, 1934

Microgale pulla Jenkins, 1988

HOLOTYPE—MCZ 45465: juvenile male, body in alcohol, skull extracted, collected by M. Drouhard.

TYPE LOCALITY—Environs of Diego-Suarez (Antsiranana, ca. 12°16'S, 49°18'E; see MacPhee, 1987. Probably Montagne d'Ambre; see Jenkins et al., 1997).

REFERRED MATERIAL—FMNH 156456, 156585, 156586: 8 km NW of Eminiminy, 24°37'S, 46°45'E, 440 m; FMNH 156457, 156458: 12.5 km NW of Eminiminy, 24°35'S, 46°44'E, 810 m; FMNH 156587, 156588, UA-SMG 7543: 13.5 km NW of Eminiminy, 24°35'S, 46°44'E, 1200 m; FMNH 156459, 156589: 15 km NW of Eminiminy, 24°34'S, 46°43'E, 1500 m; FMNH 156590: 20 km SE of Andranandambo, 24°33'S, 46°43'E, 1875 m.

KEY FEATURES—Very small, TL slightly shorter than HB. Dorsal pelage dark brown, ventral pelage dark gray-brown, tail uniform dark gray. Skull very small and delicate, rostrum slender, braincase shallow and long, occipital condyles posterodorsally orientated. Diastemata between I1 and I2, on either side of C and P2, and between c and p2; anterior and posterior accessory cusps present on

TABLE 13-4. Capture results for small mammals trapped in pitfall lines in the humid forest of parcel 1 (440, 810, 1200, 1500, and 1875 m) and the spiny bush of parcel 2 (120 m) of the RNI d'Andohahela.

Character	Line					
	1	2	3	4	5	6
Descriptive information						
Forest type	Lowland 440 m			Transitional lowland/montane 810 m		
Altitude (m)	420	430	440	800	830	840
Line placement†	V	S	R	V	S	R
First sample day (day/month)	20/10	20/10	20/10	29/10	29/10	29/10
Last sample day (day/month)	26/10	26/10	26/10	5/11	5/11	5/11
Total pitfall nights	77	77	77	88	88	88
Species sampled						
MAMMALIA						
Insectivora						
<i>Tenrec ecaudatus</i>	—	—	—	—	—	—
<i>Microgale cowani</i>	—	—	—	—	—	—
<i>M. dobsoni</i>	—	1	—	—	—	—
<i>M. fotsifotsy</i>	—	2	—	—	—	—
<i>M. gracilis</i>	—	—	—	—	—	—
<i>M. gymnorhyncha</i>	—	—	—	—	—	—
<i>M. longicaudata</i>	—	1	—	2	2	1
<i>M. parvula</i>	1	2	—	—	2	—
<i>M. principula</i>	3	1	1	—	—	2
<i>M. soricoides</i>	—	—	—	1	—	—
<i>M. thomasi</i>	3	2	—	1	1	2
<i>Oryzorictes hova</i>	—	—	—	—	—	—
<i>Geogale aurita</i>	—	—	—	—	—	—
<i>Suncus madagascariensis</i>	—	—	—	—	—	—
Rodentia						
<i>Eliurus</i> spp.	—	—	1	—	—	1
Capture results						
Total number of small mammal captures	7	9	2	4	5	6
Total number of <i>Microgale</i> captures	7	9	1	4	5	5
Total number of Insectivora species	3	6	1	3	3	3
Total number of <i>Microgale</i> species	3	6	1	3	3	3
Capture rate of <i>Microgale</i>	9.1%	11.7%	3.3%	4.5%	5.7%	5.7%

* The site in the spiny bush lacked the topographical relief found in parcel 1 humid forest, and the designation of the position categories is slightly exaggerated.

† V = valley; S = slope; R = ridge.

I2, I3, and P2; talonid of m3 with well-developed hypoconulid but reduced hypoconid, entoconid, and entoconid ridge, and narrow, shallow talonid basin.

MEASUREMENTS—External and cranial measurements are presented in Table 13-3.

POPULATION STRUCTURE AND REPRODUCTION—The sex ratio of females to males was 1:1.5. The ratio of juveniles to adults was 1:1. The anterior dentition of all juveniles was completely deciduous, with all molars erupted. One adult female was lactating. Mammary formula: 1-0-2 (n = 2).

REMARKS—This species is now known to occur

in a variety of forested localities ranging from the RNI d'Andohahela in the south to PN de la Montagne d'Ambre in the far north (Raxworthy & Nussbaum, 1994; Goodman et al., 1996a; Jenkins et al., 1997). It has also been recorded in anthropogenic habitats, including isolated and fragmented small forest blocks (Goodman et al., 1996b). In the RNI d'Andohahela (parcel 1) it was recorded across the complete elevational range of the transect from 440 to 1875 m. At other sites surveyed along elevational gradients, this species also tends to be captured in pitfall buckets in relatively low numbers across a broad altitu-

TABLE 13-4. *Extended.*

Line											
7	8	9	10	11	12	13	14	15	16	17	18
Montane 1200 m			Montane 1500 m			Upper montane sclerophyllous 1875 m			Spiny bush 120 m*		
1225 R	1200 V	1215 S	1500 V	1500 S	1550 R	1890 V	1900 R	1825 S	130 S	120 R	110 V
7/11	7/11	7/11	17/11	18/11	18/11	27/11	27/11	28/11	8/12	8/12	8/12
15/11	15/11	15/11	25/11	25/11	25/11	3/12	3/12	3/12	13/12	13/12	13/12
99	99	99	99	88	88	77	77	66	66	66	66
—	2	—	—	—	—	—	—	—	—	—	—
2	2	1	7	14	12	20	42	15	—	—	—
—	—	—	1	1	4	1	4	1	—	—	—
1	—	—	—	1	—	—	—	—	—	—	—
—	—	—	—	—	1	4	1	—	—	—	—
—	—	—	1	1	—	1	—	1	—	—	—
—	—	3	3	1	1	12	5	8	—	—	—
1	1	1	2	—	—	—	1	—	—	—	—
—	—	1	—	—	—	—	—	—	—	—	—
—	1	—	1	2	1	1	1	1	—	—	—
1	2	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	2	5	—	—	—	—
—	—	—	—	—	—	—	—	—	3	1	3
—	—	—	—	—	—	—	—	—	2	4	1
—	—	—	—	1	—	—	—	—	—	—	—
5	8	6	15	21	19	41	59	26	5	5	4
4	6	6	15	20	19	39	54	26	0	0	0
4	5	4	6	6	5	7	7	5	2	2	2
4	4	4	6	6	5	6	6	5	0	0	0
4.0%	6.1%	6.1%	17.0%	22.7%	21.6%	50.1%	70.1%	39.4%	0.0%	0.0%	0.0%

dinal range (Raxworthy & Nussbaum, 1994; Goodman et al., 1996a; Goodman & Jenkins, 1998).

Another similarly sized species, *Microgale pusilla*, is not known to occur sympatrically with *M. parvula* at any site. The former species also has a broad distribution, occurring across much of the eastern humid forest and at a variety of elevations (MacPhee, 1987). The only record we are aware of for *M. pusilla* in extreme southeastern Madagascar is a specimen (USNM 578862) collected in the littoral forest of Manafiafy (24°47'S, 47°12'E). This site is within about 35 km of those in the RNI d'Andohahela in which *M. parvula* was collected, and on the basis of current information, these two allopatric species apparently

have a complicated patchwork distributional pattern.

Microgale principula Thomas, 1926

Microgale sorella Thomas, 1926: MacPhee, 1987

HOLOTYPE—BM (NH) 25.8.3.15: adult female, body in alcohol, skull extracted, collected by C. Lamberton.

TYPE LOCALITY—Midongy du Sud, SE Madagascar (Midongy Atsimo, 23°35'S, 47°01'E; see MacPhee, 1987).

REFERRED MATERIAL—FMNH 156453, 156460, 156461, 156575, 156577: 8 km NW of Emini-

TABLE 13-5. Summary of capture results for insectivores trapped in pitfall lines in the humid forest (parcel 1) and spiny bush (parcel 2) of the RNI d'Andohahela.

Species	Elevation (m)					
	Parcel 2 120	Parcel 1				
		440	810	1200	1500	1875
<i>Geogale aurita</i>	7					
<i>Suncus madagascariensis</i>	7					
<i>Microgale principula</i>		5	2	1		
<i>M. thomasi</i>		2	4	2		
<i>M. fotsifotsy</i>		2			1	
<i>M. longicauda</i>		1	5	3	5	23
<i>M. parvula</i>		2	2	2		1
<i>Tenrec ecaudatus</i>				1		
<i>M. cowani</i>				3	26	73
<i>M. soricoides</i>			1	1	3	3
<i>M. dobsoni</i>					5	4
<i>M. gracilis</i>					1	4
<i>M. gymnorhyncha</i>					2	2
<i>Oryzorictes hova</i>						6
Total specimens captured	14	12	14	13	43	116
Total <i>Microgale</i> captured	0	12	14	12	43	110
Total species captured	2	5	5	7	7	8
Capture success	7.1%	6.1%	7.1%	6.6%	21.7%	58.6%

The capture rate is standardized for the first 6 nights that three pitfall lines (11 buckets each) were in place within each elevational zone.

miny, 24°37'S, 46°45'E, 440 m; FMNH 156454, 156591: 12.5 km NW of Eminiminy, 24°35'S, 46°44'E, 810 m; FMNH 156592: 13.5 km NW of Eminiminy, 24°35'S, 46°44'E, 1200 m.

KEY FEATURES—Medium sized, TL very long, more than twice as long as HB; distal portion of tail naked and transversely wrinkled on dorsal surface; fifth hind digit elongated, subequal in length to second digit. Pelage distinctly bicolored, reddish brown dorsally, gray with buff wash ventrally. Skull medium in size, rostrum moderately short and broad, braincase moderately narrow. Short diastemata between I1 and I2, and on either side of C and P2, with I2 and I3 more or less in contact; well-developed anterior and posterior accessory cusps present on I2, C, and P2; I1 greater in crown height than C; P4 distinctly greater in crown height than P3; p2 moderately caniniform; talonid of m3 with low hypoconid, well-developed hypoconulid, broad talonid basin, reduced entoconid ridge, and entoconid absent.

MEASUREMENTS—External and cranial measurements are presented in Table 13-3.

POPULATION STRUCTURE AND REPRODUCTION—The sex ratio of females to males was 1:4. The ratio of juveniles to adults was 1:1.7. The anterior dentition of all three juveniles was fully decidu-

ous. The testes of one adult male (FMNH 156592) measured 6 × 4 mm, with convoluted epididymides. Mammary formula: 1-0-2 (n = 1).

REMARKS—One specimen was trapped 1 m above the ground on a 4-cm-diameter horizontal branch in a vine tangle, although most others were collected in pitfall traps. As mentioned under the species account for *Microgale longicauda*, *Microgale principula* was more common in the 440 m zone than at higher altitudes. On the basis of our trapping results, the upper elevational limit of this species is approximately 1200 m. It is known from a variety of sites in the eastern humid forest from the RNI d'Andohahela north to at least the RS d'Anjanaharibe-Sud (Goodman & Jenkins, 1998).

Microgale soricoides Jenkins, 1993

HOLOTYPE—BM (NH) 91.565: adult male in alcohol, skull extracted, collected 13 April 1991 by Christopher J. Raxworthy.

TYPE LOCALITY—Mantady National Park, ca. 15 km N of Périnet (Andasibe), 18°51'S, 48°27'E, in primary rain forest, 1100–1150 m.

REFERRED MATERIAL—FMNH 156594: 12.5 km

NW of Eminiminy, 24°35'S, 46°44'E, 810 m; FMNH 156462, 156583, 156595: 13.5 km NW of Eminiminy, 24°35'S, 46°44'E, 1200 m; FMNH 156463–156465, 156596: 15 km NW of Eminiminy, 24°34'S, 46°43'E, 1500 m; FMNH 156466, 156467, 156597, UA-SMG 7668, 7676, 7683: 20 km SE of Andranandambo, 24°33'S, 46°43'E, 1875 m.

KEY FEATURES—Size large, TL subequal to or longer than HB. Pelage light buff brown dorsally, gray-brown ventrally with reddish buff wash. Skull moderately large and robust, rostrum and interorbital region broad, braincase short and broad; supraoccipital ridge present. First upper I1 markedly robust and proodont; i1 and i2 robust and procumbent, i2 smaller than i1 but larger than c; first upper and lower premolars very small, with a single root; talonid of m3 reduced to very low hypoconid, oblique crest, and prominent hypoconulid.

MEASUREMENTS—External and cranial measurements are presented in Table 13-3.

VARIATION—The early replacement of the first upper incisor, described below, may be abnormal. There are, however, indications from other populations that this eruption sequence, atypical for most species of *Microgale*, is the norm for this species. Specimens from RNI d'Andohahela are smaller on average than those collected from sites further north in Madagascar (see Jenkins, 1993; Jenkins et al., 1996; Goodman & Jenkins, 1998).

POPULATION STRUCTURE AND REPRODUCTION—Of the adults in this small sample only females were collected. The ratio of juveniles to adults was 1:4. In both juveniles, the anterior dentition, with the exception of I1, was deciduous, but M3 and m3 in one specimen were still in the process of erupting. Two of the adult females were pregnant and three were lactating. Mammary formula: 0-1-2 (n = 1), 0-2-1 (n = 2), 1-0-2 (n = 2), 1-1-2 (n = 3).

REMARKS—Most specimens were caught on the ground in Sherman or pitfall traps, although one was trapped 2 m above ground on a 2-cm-diameter horizontal liana that ran from the ground to a height of 7 m.

This recently described species is broadly distributed in the eastern humid forest; it is known to occur in a variety of sites from the RNI d'Andohahela north to at least the RS d'Anjanaharibe-Sud, including RNI d'Andringitra and PN de Mantady (Jenkins, 1993; Goodman et al., 1996c; Goodman & Jenkins, 1998).

Microgale thomasi Major, 1896

HOLOTYPE—BM (NH) 97.9.1.108: adult male; skin, skull, and skeleton, collected 19 July 1895 by C. I. Forsyth Major.

TYPE LOCALITY—Ampitambe Forest (The position of this locality has never been satisfactorily fixed, although the best estimate to date is that proposed by Carleton & Schmidt, 1990, in Fianarantsoa Province at ca. 20°22'S, 47°46'E, >900 m.).

REFERRED MATERIAL—FMNH 156472–156478: 8 km NW of Eminiminy, 24°37'S, 46°45'E, 440 m; FMNH 156353, 156354, 156479–156481, 156599, 156600: 12.5 km NW of Eminiminy, 24°35'S, 46°44'E, 810 m; FMNH 156482–156484: 13.5 km NW of Eminiminy, 24°35'S, 46°44'E, 1200 m.

KEY FEATURES—Moderately large *Microgale* (see Table 13-3). TL shorter than HB, ears moderately prominent. Dorsal pelage speckled dark rufous brown, paler ventrally; tail bicolored at least proximally in most specimens, dark brown dorsally, buff ventrally, with moderately long, dense scale hairs. Skull moderately robust, braincase deep, short and broad; basisphenoid stepped between anterior ends of tympanic bullae. First upper and lower premolars large; hypoconid of m3 prominent, entoconid and entoconid ridge present, talonid basin well marked.

MEASUREMENTS—External and cranial measurements are presented in Table 13-3.

POPULATION STRUCTURE AND REPRODUCTION—The sex ratio of females to males was 1:2. The ratio of juveniles to adults was 1:1.8. The juveniles showed variation in dental development; in one the anterior dentition was fully deciduous, in another i3 was erupting, in a third I1 and I3 were erupting, and in the fourth all the permanent anterior teeth were erupting or had erupted, with the exception of the second deciduous upper and lower premolars (dP3 and dp3). One adult female was lactating and one juvenile female (FMNH 156482) with deciduous dentition was pregnant with one embryo in each oviduct. Conversely, one male with a fully permanent dentition (FMNH 156600) was reproductively immature with non-convoluted epididymides. Mammary formula: 0-1-2 (n = 1), 0-2-1 (n = 1), 0-2-2 (n = 1).

REMARKS—Prior to the recent wave of biological inventories on Madagascar, *Microgale thomasi* was poorly known in museum collections and seemed to be restricted to the southern portion of the eastern humid forest (MacPhee, 1987). In the humid forests of the RNI d'Andohahela this species was

relatively common from low to mid-altitudes. It was also commonly captured with pitfall techniques in the Marosohy Forest, along the northeastern boundary trail of parcel 1 of the RNI d'Andohahela (USNM 578772–578783). It is also known to occur in and around the PN de Ranomafana (USNM 448876, 448877, 448917, 449193–449196). The northern limit of this species is apparently the Périnet area (Heim de Balsac, 1972), and it is also known from the humid forests to the east and northeast of Ambositra (Ampitambe and Ivohimanitra). *Microgale monticola*, a species morphologically similar to *M. thomasi*, occurs further north, in the vicinity of the RS d'Anjanaharibe-Sud and within the elevational range of 1550–1950 m (Goodman & Jenkins, 1998). *Microgale thomasi* and *M. monticola* are believed to be allopatric.

Family Soricidae

Suncus madagascariensis (Coquerel, 1848)

HOLOTYPE—MNHN no. 96: unsexed mounted specimen, skull removed and subsequently lost, brought back to France by M. Coquerel in 1847, collection date unknown (Rode, 1942).

TYPE LOCALITY—Nossi-Bé (= Nosy Be).

REFERRED MATERIAL—FMNH 156493, 156494, 156604, 156605: 7.5 ENE of Hazofotsy, 24°49'S, 46°36'E, 120 m.

KEY FEATURES—Extremely small (see Table 13-1). Pelage soft and short; tail with long, fine-bristle hairs. Skull very small and delicate; rostrum short and narrow; interorbital region narrow, short; braincase relatively long, shallow, and broad. Dental formula 3/1 1/0 2/2 3/3 = 30 (nomenclature of anterior unicuspid dentition unresolved); I1 well developed, proodont, principal cusp hook-shaped; upper unicuspid decrease in size from moderately large anteriormost (I2) to very small fourth unicuspid; talon of P4 broad; cusp pattern of trigon M2 and M3 dilambodont, M3 anteroposteriorly compressed; i1 large, procumbent; c absent; first lower unicuspid small, second lower unicuspid approximately half height of m1; m3 talonid reduced to a single cuspid but talonid basin present.

MEASUREMENTS—External measurements are presented in Table 13-1.

POPULATION STRUCTURE AND REPRODUCTION—All specimens collected were male; two of these (FMNH 156604 and 156605) had convoluted ep-

ididymides measuring respectively 3×2 and 4×2 mm.

REMARKS—All specimens were collected in slightly disturbed spiny forest using pitfall traps.

The taxonomic status of this form is unclear. Heim de Balsac and Meester (1977) tentatively placed this animal as a subspecies of *Suncus etruscus*, but more recently Hutterer (1993) elevated it to a species. It is uncertain if this animal was introduced to Madagascar or is part of the native fauna. If it was introduced, the origin of the founding population is unknown. These questions are probably best resolved with biochemical and karyotypic studies.

Analysis and Discussion

General

A total of 1,254 pitfall bucket-days was accrued during the survey of the RNI d'Andohahela between 26 October and 13 December 1995. These were divided between the two habitat types as 231 bucket-days at 440 m, 264 at 810 m, 297 at 1200 m, 275 at 1500 m, and 220 at 1875 m in the humid forest (parcel 1), and 198 bucket-days at 120 m in the spiny forest (parcel 2) (Tables 13-4 and 13-5). There were 233 small mammals captured in parcel 1, including 220 *Microgale*, seven *Oryzorictes*, two *Tenrec*, and three species of *Eliurus* (for rodents, see Chapter 14). Fourteen small mammals were caught in parcel 2, including seven individuals each of *Geogale aurita* and *Suncus madagascariensis*. Furthermore, 4,573 trap-nights were accrued in the humid forest using small mammal traps with a standard baiting regime (Chapter 14), and 27 (0.60 %) lipotyphlans were captured. After 685 trap nights in the spiny bush, one (0.15 %) tenrecine was caught. The following species were obtained in standard museum traps: parcel 1—*Microgale dobsoni*, *M. gymnorhyncha*, *M. principula*, *M. soricoides*, *M. thomasi*, *Oryzorictes hova*, and *Setifer setosus*; parcel 2—*Echinops telfairi*. All species of *Microgale* recorded within each elevational zone were captured in the pitfall traps, and no species was taken exclusively in the small mammal traps. The single exception was an individual of *M. dobsoni* caught at 1200 m; this constituted our single record for the species within that elevational zone.

The combined trapping results, with pitfalls and standard live traps, located 15 species of *Tenre-*

cidae (*Echinops*, *Setifer*, *Tenrec*, *Geogale aurita*, *Oryzorictes hova*, and 10 species of *Microgale*) and one species of Soricidae (*Suncus madagascariensis*) within the RNI d'Andohahela. The only lipotyphlans previously documented from the reserve are *Tenrec* and *Setifer* (O'Connor et al., 1987; Nicoll & Langrand, 1989). Before proceeding with the analysis of the trapping results, it is important to establish whether the sampling effort was sufficient to reflect some measure of completeness for the survey and the actual lipotyphlan species richness within each elevational zone.

Species Accumulation Curves

The total number of species known from each elevational zone was plotted as a function of sampling effort (33 pitfall buckets per 24-hr period) to produce species accumulation curves (Fig. 13-1a). An examination of these curves shows that the accumulation of previously unrecorded species was slow in the 440 m zone, and by the end of the sampling period a plateau had not been reached. This pattern is in contrast to those from virtually all of the other elevational zones sampled in parcel 1; an asymptote was reached in the 810 m zone after 66 pitfall bucket-days (total of five species in 264 pitfall bucket-days), in the 1200 m zone after 231 pitfall bucket-days (total of eight species in 297 pitfall bucket-days), in the 1500 m zone after 264 pitfall bucket-days (total of eight species in 297 pitfall bucket-days), and in the 1875 m zone after 154 pitfall bucket-days (total of eight species in 220 pitfall bucket-days). In the spiny bush (parcel 2) the plateau in the species accumulation curve was reached after 2 nights of pitfall operation (total of two species in 198 bucket-days). In both parcels 1 and 2 the flattening of the species accumulation curve within each elevational zone that occurred with additional trapping effort did not generally coincide with a decline in overall pitfall trap success (Fig. 13-1b). The number of lipotyphlans captured within each elevational zone did tend to decline, however, during the time the lines were in place.

We feel that our overall trapping results, particularly with pitfall techniques, closely parallel the actual species richness of lipotyphlans within each elevational zone. (For further discussion of this point see Goodman & Jenkins, 1998, p. 155.) The only species that has been previously documented from the immediate region of the RNI d'Andohahela and was not encountered during the

1995 survey is *Microgale talazaci*. This animal has been collected in the Nahampoana Forest, from a site resting on lateritic soils at 100 m (USNM 577053–57) and in the Marosohy Forest, between 700 and 725 m, along the northeastern boundary of parcel 1 of the RNI d'Andohahela (USNM 578746, 578747). Given these records we assume that it also occurs within parcel 1 of the RNI d'Andohahela, but was not captured in our trapping devices. An additional species, *Hemicentetes*, was previously reported as possibly occurring in the reserve (O'Connor et al., 1987). Other studies of the Malagasy Lipotyphla using pitfall traps indicate that this technique is effective for documenting species richness in eastern humid forest (Raxworthy & Nussbaum, 1994; Goodman et al., 1996c).

Trapping Success and Abundance

Summary information on the pitfall trapping is given in Tables 13-4 and 13-5. Three pitfall lines were in operation within each elevational zone for a minimum of 6 days, and there was considerable variation in the capture rate of lipotyphlans within and between lines. For *Microgale* in humid forest the capture success rate at 440 m varied from 3.3% to 11.7% (average 6.1%), at 810 m from 4.5% to 5.7% (average 7.1%), at 1200 m from 4.0% to 6.1% (average 6.6%), at 1500 m from 17.0% to 22.7% (average 21.7%), and at 1875 m from 39.4% to 70.1% (average 58.6%). In the spiny forest portion of parcel 2 the capture success rate for the single site sampled (120 m) varied from 6.1% to 7.6% (average 7.1%).

At the 1500 and 1875 m sites in the RNI d'Andohahela, the pitfall capture success was exceptionally high. In the PN de la Montagne d'Ambre, capture rates of comparable magnitude (range 60.6–77.9%) have been reported for an area of montane forest between 1300 and 1380 m, just below the summit (1475 m) of the mountain (Goodman et al., 1996a). At lower elevations on the same mountain, capture rates as high as 50.4% have been calculated for 1250 m in mid-montane forest and between 55.8% and 58.4% in the 980–1010 m zone (Raxworthy & Nussbaum, 1994; Goodman et al., 1996a).

Relationship Between Rainfall and Capture Rates

During the course of numerous field seasons in Madagascar trapping lipotyphlans with pitfall

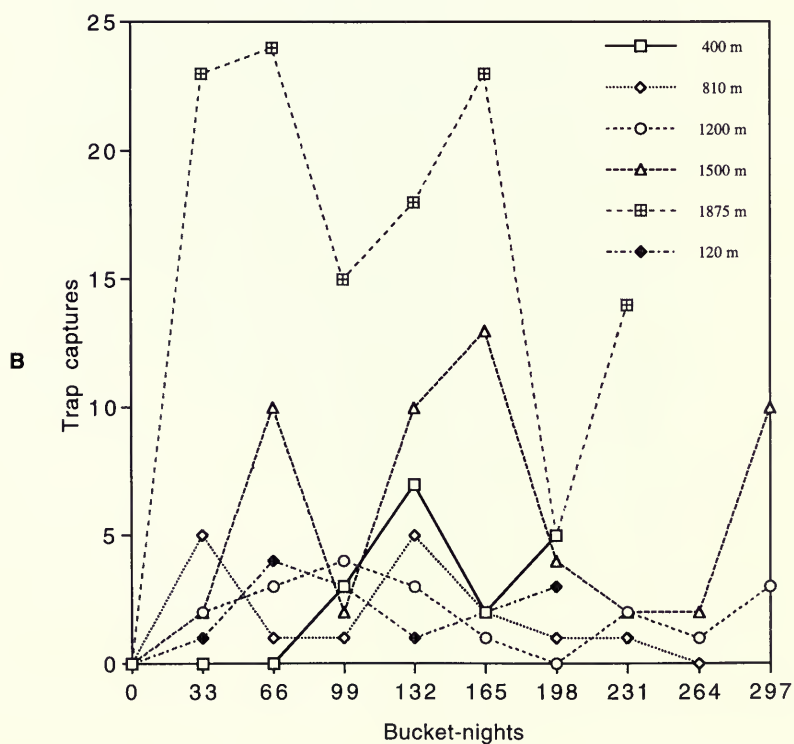
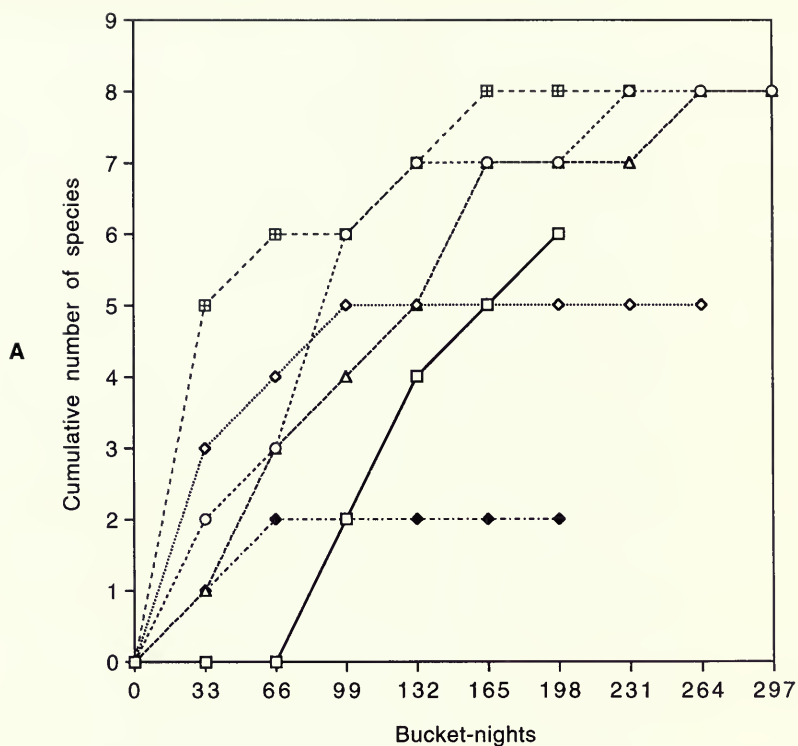


FIG. 13-1. Species accumulation curves (A) and pitfall trap success (B) plotted for each elevational zone in the RNI d'Andohahela against the total number of bucket-nights. The pitfall lines placed in parcel 2 (spiny bush) were

techniques it has been our impression that capture rates are higher after rainfall. To determine whether there was a relationship between these variables during the RNI d'Andohahela survey, a series of Kendall's rank correlations was computed for each elevational zone, with the y variable being the number of animals captured and the x variable the amount of precipitation during the previous 24 hr. This procedure mirrors that used by Goodman et al. (1996c) to evaluate the same relationship in the RNI d'Andringitra.

In the RNI d'Andohahela no significant correlation was found between capture rate and rainfall. The next stage in the analysis was to perform a regression analysis for each elevational zone using the same variable configuration as in Kendall's rank correlations. In all cases there was a positive trend between rainfall and capture rates, but the results were not statistically significant. In general there was little rainfall during the inventory, particularly at the 440, 810, and 1200 m sites (see Chapter 1). Perhaps if the inventory had been slightly later in the year and during the principal rainy season (usually starting in December) there would have been a stronger correlation between these variables.

Scansoriality in Species of *Microgale*

Using morphometric correlations associated with tail, body, and hind foot measurements, Eisenberg and Gould (1970) divided *Microgale* species into four locomotor forms: fossorial or semifossorial; surface foragers with moderate climbing ability; surface foragers and climbers; and climbers and springers. Because our principal method of trapping lipotyphlans was the use of pitfall buckets, which only capture species moving along the ground, much of our information could not be used to address the question of adaptations toward arboreality in this group. About 40% of the small mammal traps were installed above the ground within each elevational zone, however, and 4,395 trap-nights were accrued (see Chapter 14); these data are relevant to the question of arboreality in *Microgale*.

Single individuals of three *Microgale* species were captured in mammal live traps. A specimen

of *M. principula* was obtained on a 4-cm-diameter horizontal branch running through vine tangle and 1 m off the ground. This long-tailed species, which Eisenberg and Gould (1970) placed in their climbers and springers class, had been noted previously to have prehensile tail adaptations (Thomas, 1926). Although this species and *M. longicaudata* show modifications of the tail for prehensile use (Goodman & Jenkins, 1998), the vast majority of the *M. principula* and all of the *M. longicaudata* animals captured in the RNI d'Andohahela were in pitfall buckets. Thus, these two species spend considerable time moving on the ground. One *M. dobsoni* was obtained 2.5 m above ground on a 3-cm-diameter horizontal branch. This relatively short-tailed species had been classified previously as having moderate climbing ability (Eisenberg & Gould, 1970). An individual of the moderately long-tailed species *M. soricoides* was trapped 2 m above the ground on a 2-cm-diameter horizontal liana that extended from ground level to about 7 m. TL/HB in this species is 1.2 ± 0.09 ($n = 12$, range 1.0–1.3), and HF/HB is 0.22 ± 0.01 ($n = 12$, range 0.20–0.23); these values would place it in Eisenberg and Gould's (1970) class of animals with climbing ability. Although there are few data available on arboreality in the Tenrecidae, no species is known to live exclusively off the ground.

Altitudinal Variation Within Parcel 1

On the basis of the trapping regimens used during the survey, we are able to present some details on the elevational ranges of the various Lipotyphla found in parcels 1 and 2 of the RNI d'Andohahela (Table 13-6). *Setifer setosus* was found only in lowland forest, at an altitude of 440 m, whereas *Tenrec ecaudatus* was observed or trapped between 440 and 1200 m. Species of *Microgale* were found at all altitudes within the different types of humid forest. *M. principula* and *M. thomasi* were documented in lowland, transitional, and montane forest between 440 and 1200 m, with more specimens of both species collected at the lower altitudes. Only two species, *M. longicaudata* and *M. parvula*, were found at all altitudes and forest types from 440 to 1875 m. *Mi-*

←

at 120 m and those in parcel 1 (humid forest) at 440, 810, 1200, 1500, and 1875 m. Information from the three lines at each zone is combined.

TABLE 13-6. The known elevational distribution of Lipotyphla in the humid forest (parcel 1) and spiny bush (parcel 2) of the RNI d'Andohahela.

Species	Elevation (m)					
	Parcel 2 120	Parcel 1				
		440	810	1200	1500	1875
<i>Geogale aurita</i>	x					
<i>Suncus madagascariensis</i>	x					
<i>Echinops telfairi</i>	x					
<i>Setifer setosus</i>		x				
<i>Microgale principula</i>		x	x	x		
<i>Microgale thomasi</i>		x	x	x		
<i>Microgale fotsifotsy</i>		x	[x]	x	x	
<i>Microgale longicaudata</i>		x	x	x	x	x
<i>Microgale parvula</i>		x	x	x	x	x
<i>Tenrec ecaudatus</i>		S	x	x		
<i>Microgale cowani</i>				x	x	x
<i>Microgale soricoides</i>			x	x	x	x
<i>Microgale dobsoni</i>		x	[x]	x	x	x
<i>Microgale gracilis</i>					x	x
<i>Microgale gymnorhyncha</i>					x	x
<i>Oryzorictes hova</i>				x*		x
Total number of species	3	8	8	9	8	8
Total number of <i>Microgale</i>	0	6	7	8	8	7

Information is based on all trapping techniques. Inferred occurrence within an elevational swath [in brackets] is based on the presence of a species in the zones above and below the one in question. Sight records are designated with the letter S.

* The only record of this species in the 1200 m zone was an individual recovered from the digestive system of a snake (see text p. 193). This record is not included in the species total for the 1200 m zone.

Microgale longicaudata was considerably more abundant in transitional upper montane/sclerophyllous forest, at 1875 m (63.2%), than in lowland forest, at 440 m (2.7%), based on pitfall captures. *Microgale cowani* and *M. soricoides* occurred from transitional lowland/montane forest at 810 m to transitional upper montane/sclerophyllous forest at 1875 m. Both species were also most abundant at higher altitudes. In *M. cowani* 71.6% of the specimens captured in pitfalls during the survey were obtained at 1875 m, 24.5% at 1500 m, and 2.9% at 1200 m. *Microgale dobsoni* was found from 1200 to 1875 m, whereas both *M. gracilis* and *M. gymnorhyncha* were collected only at the highest altitudes, from 1500 to 1875 m. *Microgale fotsifotsy* was the only species apparently showing a disjunct distribution, with very small samples collected at 410, 1200, and 1500 m; this is attributed to a sampling anomaly. *Oryzorictes hova* was collected only at 1875 m.

Habitat Separation

As defined by numerous proposed systems for the vegetational classification of Madagascar (re-

viewed by Lowry et al., 1997; see Chapter 2), the two parcels of the RNI d'Andohahela investigated during this study are floristically different. Regardless of the names applied to these two habitat types, parcel 1 can be characterized as humid (rain) forest and parcel 2 as xerophytic bush. Between the two parcels, which are separated by a distance of about 20 km, there is a remarkable change in the climate and flora across the rain shadow of the Anosyenne Mountains. Rain systems moving in from the eastern coast of Madagascar release their precipitation along the eastern slopes of the Anosyenne Mountains, and as Donque (1972, p. 136) has noted, "the boundary between the semi-arid climate and the tropical damp climate of the south-east coast is extremely sharp." This ecotone between wet and dry is known to be a major barrier to dispersal for certain groups of land vertebrates (Goodman et al., 1997).

Tenrec ecaudatus, *Oryzorictes hova*, and all species of *Microgale* were taken only in the humid forest of parcel 1, and *Echinops telfairi*, *Geogale aurita*, and *Suncus madagascariensis* were captured only in the spiny forest of parcel 2. We found no species in common between parcel 1 and

TABLE 13-7. Faunal similarity coefficients for Lipotyphla communities in the various altitudinal and ecological zones of parcels 1 (120 m) and 2 (440, 810, 1200, 1500, and 1875 m) in the RNI d'Andohahela.

	120 m	440 m	810 m	1200 m	1500 m	1875 m
120 m	—	0.0	0.0	0.0	0.0	0.0
440 m	0.0	—	0.88	0.88	0.50	0.38
810 m	0.0	0.78	—	1.0	0.63	0.50
1200 m	0.0	0.70	0.89	—	0.75	0.63
1500 m	0.0	0.33	0.45	0.55	—	0.88
1875 m	0.0	0.23	0.33	0.42	0.78	—

The similarity coefficients derived from Simpson's Index are above the diagonal; those derived from the Jaccard Index are below the diagonal.

2 of the reserve. The only possible exception to this statement is *Tenrec ecaudatus*, which has been reported from both parcels 1 and 2 (O'Connor et al., 1987). The western versant of the Anosyenne Mountains, along the abrupt gradient passing westward from wet to dry, thus appears to represent a dramatic barrier to dispersal and mixing of the lipotyphlan faunas within these two parcels.

Despite the modern dramatic faunal turnover along the western slopes of the Anosyenne Mountains, this boundary (or at least the site of the boundary) was not constant over recent geological time, and there have been marked fluctuations in the regional biological communities. The Grotte d'Andrahomana, a well-known Holocene subfossil cave site in the region, is located about 50 km west-southwest of Tolagnaro in a region that is now largely spiny bush. This site, which was excavated in the early portion of this century (Grandidier, 1902; Goodman & Rakotondravony, 1996), contained a rich assortment of vertebrate material. Among these remains were many species of extinct and extant lemurs, some with affinities to the humid forest and others to the dry forest (Godfrey et al., 1997). The type specimen of *Microgale decaryi* G. Grandidier, 1928 (a synonym of *M. principula* according to MacPhee, 1987) was excavated from this cave. The remains of an extinct rodent, *Hypogeomys australis*, whose sole extant congener lives in dry deciduous forest in the Morondava region, have been excavated from the cave as well (Grandidier, 1903). Radiocarbon dating of *Hypogeomys* remains from the Grotte d'Andrahomana shows that these animals existed in the region $4,440 \pm 60$ BP (Goodman & Rakotondravony, 1996).

Along the eastern slopes of parcel 1 the shifts in habitat between the various elevational zones are part of a continuum of vegetational change as a function of altitude and microclimate shifts. In or-

der to further assess the faunistic relationships of the lipotyphlan faunas between each of the elevational zones, we calculated two different similarity indices, Simpson's Index and the Jaccard Index:

$$\text{Simpson's Index} = \frac{C}{N_1}$$

$$\text{Jaccard Index} = \frac{C}{N_1 + N_2 - C}$$

where N_1 = the number of species at site 1 (the smaller fauna), N_2 = the number of species at site 2, and C = the number of species common to both sites. The coefficients derived from these indices, presented in Table 13-7, were used in a cluster algorithm ("Phylip," written by J. Felsenstein using the Fitch-Margoliash method with contemporary tips).

The results of the cluster analyses are presented in Figure 13-2. Both indices show the same relationship. Within the elevational zones studied in the reserve, the spiny bush region at 120 m contains a fauna that is unique with regard to the other sites in the humid forest. Three distinct groups occur in parcel 1: (1) the lipotyphlan species found in the lowland forest, at 440 m, (2) the lower montane community, between 810 and 1200 m, and (3) the upper montane to sclerophyllous forest group, between 1500 m and the summital zone at 1875 m.

Comparison Between Mountains

Over the past decade or so there has been considerable instability in the alpha-level taxonomy of the genus *Microgale*, and the number of species recognized has varied considerably (cf. MacPhee, 1987; Nicoll & Rathbun, 1990; Stephenson, 1995). Our knowledge of the geographical ranges of *Microgale* has grown substantially

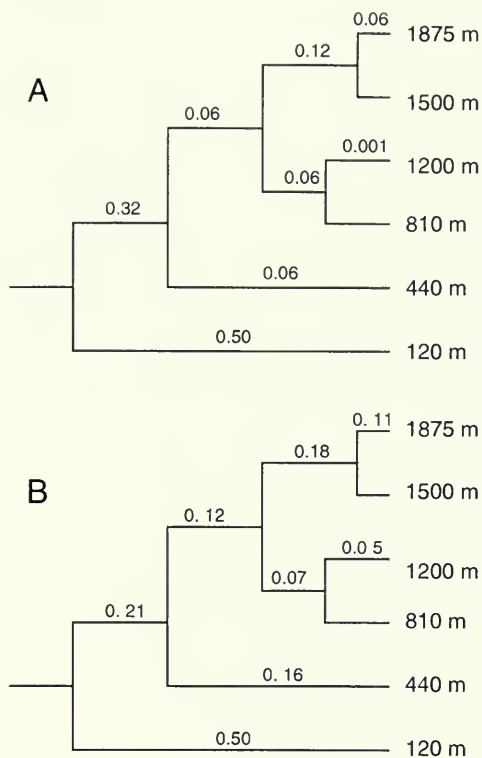


FIG. 13-2. Cluster analysis of faunal similarity of insectivore communities occurring in a range of elevational zones in parcel 1 (humid forest, sites from 440 to 1875 m) and parcel 2 (spiny bush, site at 120 m) in the RNI d'Andohahela. Simpson's Index (A), and the Jaccard Index (B) were used. The data are based on Table 13-7, which is derived from Table 13-6.

over the past few years, largely through the efforts of field surveys that involved specimen collection. The increase in research on *Microgale*—and Tenrecidae in general—has brought with it a clearer picture of species limits within this group.

With the use of comparable field techniques, direct comparisons are now possible between the lipotyphlans from the eastern humid forests of RNI d'Andringitra, RS d'Anjanaharibe-Sud, or PN de la Montagne d'Ambre and those from RNI d'Andohahela (parcel 1 only) (Table 13-8). These four localities span the complete latitudinal swath of eastern humid forests on the island. From south to north, there have been 13 lipotyphlan species (including 10 *Microgale* spp.) documented in the RNI d'Andohahela (parcel 1), 15 species (including 11 *Microgale*) in the RNI d'Andringitra (Goodman et al., 1996c; Jenkins et al., 1996; Goodman, unpubl. data), 15 species (including 11 *Microgale*) in the RS d'Anjanaharibe-Sud (Good-

man & Jenkins, 1998), and nine species (including six *Microgale*) in the PN de la Montagne d'Ambre (Raxworthy & Nussbaum, 1994; Goodman et al., 1996a; Jenkins et al., 1997). Thus, with the exception of the reduced species richness in the Montagne d'Ambre region, there is considerable consistency in the level of lipotyphlan diversity within the humid forests across the 10 degrees of latitude from Andohahela to Anjanaharibe-Sud. It is possible that the reduced species richness from Montagne d'Ambre is related to recent volcanic activity and isolation from other humid forests in recent geological times (Goodman et al., 1996a).

On the basis of our current knowledge with regard to patterns of geographical variation and *Microgale* species limits, a number of generalizations can be made. Several animals are found across a vast area of the eastern humid forest from Andohahela to Anjanaharibe-Sud (those species whose names are followed by an asterisk occur north to Montagne d'Ambre): *M. cowani*, *M. dobsoni*, *M. fotsifotsy*,* *M. gymnorhyncha*, *M. longicaudata*,* *M. parvula*,* and *M. soricoides*. Other species are known from the southern portion of the humid forest zone: *M. gracilis*, *M. principula*, and *M. thomasi*; and some are known from the northern portion of this zone: *M. breviceaudata* and *M. talazaci*. One species, *M. taiva*, appears to be centrally distributed. *Microgale drouhardi* has an apparently discontinuous distribution, based on the sites sampled. Finally, two species, *M. dryas* and *M. monticola*, apparently have limited geographical ranges.

Relationships Between Species Richness and Abundance

The data from these four sites allow further elaboration of the relationships among *Microgale* species richness, density, and variation along elevational and latitudinal gradients. Numerous hypotheses have been presented to explain patterns of diversity along gradients (e.g., Brown, 1988; Colwell & Hurtt, 1994; Rosenzweig, 1995; Rahbek, 1997). One that has received considerable attention is that changes in species richness along elevational gradients closely mirror environmental productivity (Ricklefs & Schluter, 1993; Rosenzweig, 1995). For tropical forests there is evidence that productivity is highest at mid-elevations (Janzen et al., 1976).

Our purpose here is not to test this hypothesis,

TABLE 13-8. Distribution of Lipotyphla on four different mountains in the eastern humid forest of Madagascar.

Species	Site:	RNI	RNI	RS	PN de la
	Elevational range (m):	d'Andohahela*	d'Andringitra†	d'Anjanaharibe-	Montagne
	Latitude:	440–1875 m	720–2450 m	Sud‡	d'Ambre¶
		25°S	22°S	15°S	12°S
Soricidae					
<i>Suncus murinus</i> ¶					+
Tenrecidae					
<i>Hemicentetes nigriceps</i>			+		
<i>Hemicentetes</i> sp.				+	
<i>Microgale brevicaudata</i>					+
<i>Microgale cowani</i>		+	+	+	
<i>Microgale dobsoni</i>		+	+	+	
<i>Microgale fotsifotsy</i>		+	+	+	+
<i>Microgale gracilis</i>		+	+		
<i>Microgale gymnorhyncha</i>		+	+	+	
<i>Microgale longicaudata</i>		+	+	+	+
<i>Microgale drouhardi</i>			+		+
<i>Microgale dryas</i>				+	
<i>Microgale monticola</i>				+	
<i>Microgale parvula</i>		+	+	+	+
<i>Microgale principula</i>		+			
<i>Microgale taiva</i>			+	+	
<i>Microgale talazaci</i>			+	+	+
<i>Microgale thomasi</i>		+			
<i>Microgale soricoides</i>		+	+	+	
<i>Oryzorictes hova</i>		+		+	
<i>Oryzorictes tetradactylus</i>			+		
<i>Setifer setosus</i>		+	+	+	+
<i>Tenrec ecaudatus</i>		+	+	+	+
Total number of species		13	15	15	9
Total number of <i>Microgale</i> spp.		10	11	11	6

* Includes only species from parcel 1.

† Information derived from Jenkins et al. (1996), Goodman et al. (1996c), Langrand and Goodman (1997), and Goodman (unpubl. data).

‡ Information derived from Goodman and Jenkins (1998).

¶ Information derived from Raxworthy and Nussbaum (1994), Goodman et al. (1996a), and Jenkins et al., (1997).

|| Species introduced to Madagascar.

but simply to evaluate aspects of variation that may indicate nonuniform patterns within our data set (Fig. 13-3). With the exception of PN de la Montagne d'Ambre, all of these site surveys were conducted during the same season of different years. For two sites, RNI d'Andringitra (Fig. 13-3b) and RS d'Anjanaharibe-Sud (Fig. 13-3c), the species richness of *Microgale* shows clear peaks in the 1200 m zone or at mid-elevation. Furthermore, as measured by percent trap capture, *Microgale* abundance closely mirrors the mid-elevational hump in species richness. Thus species richness and small mammal densities parallel one another at these two sites at mid-latitudes in the eastern humid forest. When these same parameters are examined for the RNI d'Andohahela (Fig. 13-3a) and PN de la Montagne d'Ambre (Fig. 13-

3d), sites in the extreme south and north (respectively) of the eastern humid forest, a mid-elevational hump in species richness is not present and abundance increases as a function of altitude. There is thus no evidence in these two cases that species richness mirrors changes in abundance (Terborgh, 1977; Graham, 1990). The factors that give rise to these two different patterns along elevational gradients in Malagasy humid forest are unknown, but they may be related to variation in meteorological (temperature, cloud cover, and rainfall) patterns on slopes or along the 12° of latitude spanning the eastern humid forest, topographical features that may give rise to variation in orographic precipitation, soil types, food resources or resource diversity, effects of radiant-heat, or some aspects of productivity (Donque,

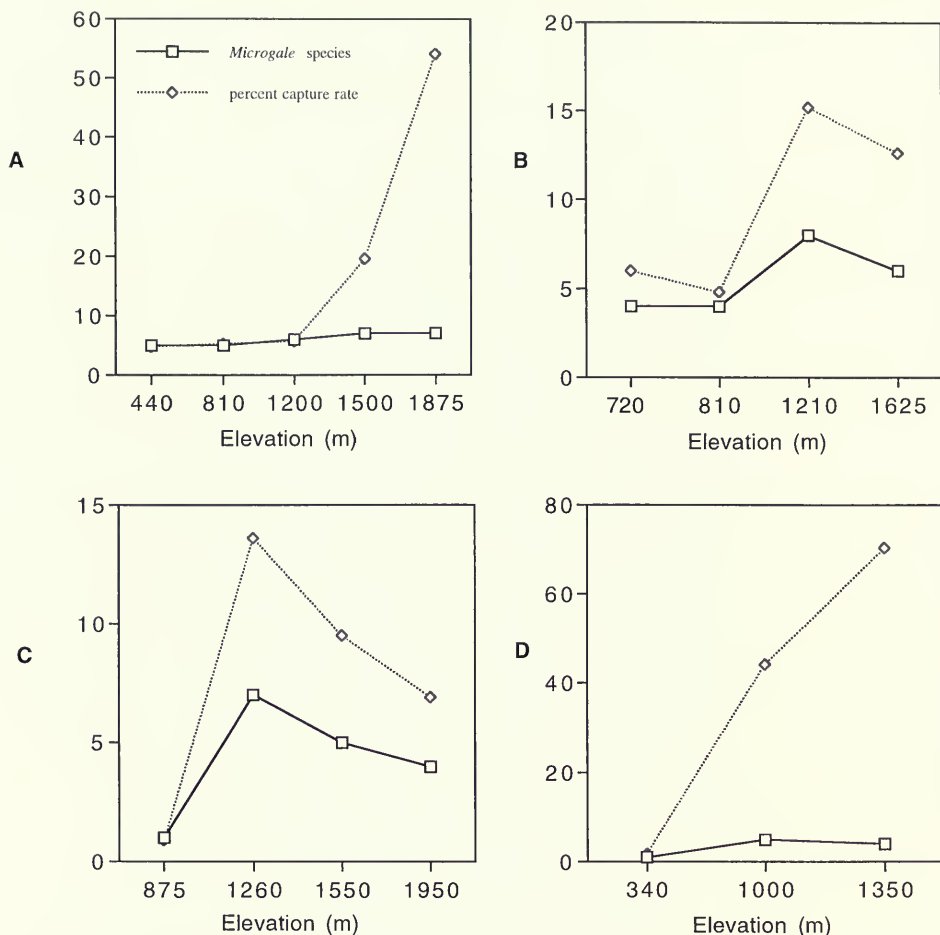


FIG. 13-3. Plots of *Microgale* species diversity and capture rates (percentage of capture) along elevational gradients at four sites on Madagascar: RNI d'Andohahela (A), RNI d'Andringitra (B), RS d'Anjanaharibe-Sud (C), and PN de la Montagne d'Ambre (D). The data are derived from the same sources mentioned in the footnotes to Table 13-8.

1972; Brown, 1973; Janzen et al., 1976; Pendry & Proctor, 1996a,b). The considerable differences that have been noted in patterns of elevational distribution between different organisms in different regions of the world may be in part related to different phylogenetic histories (Wright & Calderon, 1995; Patterson et al., in press), and thus a search for a common denominator to explain these different patterns may prove intractable.

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- ### Appendix 13-2.

2. Ratio of TL: HB > 1.7	3	
Ratio of TL: HB < 1.4	4	
3. Size smaller: HB < 67, WT < 7.9, CIL < 20.4		
..... <i>M. longicaudata</i>		
Size larger: HB > 69, WT > 9.5, CIL > 22.0		
..... <i>M. principula</i>		
4. Digits and tail tip contrastingly paler than body, tail, and feet		
..... <i>M. fotsifotsy</i>		
Tail tip and digits not obviously paler than rest of body	5	
5. Size very large: HB > 95, CIL > 30.0; i2 > c		
..... <i>M. dobsoni</i>		
Size smaller: HB < 96, CIL < 27.5; i2 subequal or > c	6	
6. Proboscis long, large rhinarium extends posterodorsally onto muzzle; forefeet broad, foreclaws enlarged	7	
		Small rhinarium confined to anterior of short proboscis; forefeet slender without lengthened foreclaws
		8
		7. Posterior region of rhinarium with transverse striae; BL < 8.0
	 <i>M. gymnorhyncha</i>
		Posterior region of rhinarium reticulated; BL > 8.5
	 <i>M. gracilis</i>
		8. I1 robust, markedly proodont; i1 >> i2 > c; P2 and p2 very small with single roots
	 <i>M. soricoides</i>
		I1 neither robust nor markedly proodont; i1 < or subequal to i2; P2 and p2 with two roots
		9
		9. Size smaller: HB < 80, WT < 16, CIL < 23.2; p2 not robust
	 <i>M. cowani</i>
		Size larger: HB > 85, WT > 19, CIL > 26.0; p2 markedly robust
	 <i>M. thomasi</i>

Chapter 14

Rodents of the Réserve Naturelle Intégrale d'Andohahela, Madagascar

Steven M. Goodman,¹ Michael D. Carleton,² and Mark Pidgeon³

Abstract

Between late October and late December 1995 a study was made of the rodents occurring in the three forested parcels that form the Réserve Naturelle Intégrale d'Andohahela. In parcel 1, composed of humid forest, five elevational zones between 440 and 1875 m were surveyed. Seven species of rodents belonging to the endemic subfamily Nesomyinae (*Eliurus majori*, *E. minor*, *E. tanala*, *E. webbi*, *Gymnuromys roberti*, *Monticolomys koopmani*, and *Nesomys rufus*), as well as a member of the introduced subfamily Murinae (*Rattus rattus*), were collected. In parcel 2, including dry spiny bush (xerophilous) and degraded riverine gallery forest, one Nesomyinae (*Eliurus myoxinus*) and *Rattus rattus* were obtained. Rodents trapped in parcel 3, a transitional forest type between humid portions of parcel 1 and dry areas of parcel 2, included *Eliurus myoxinus* and the two introduced Murinae *Rattus norvegicus* and *R. rattus*.

The highest diversity of native rodents in parcel 1 was found at 1200 m in montane forest (five species), and the lowest diversity at 440 m in lowland forest (one species) and at 1875 m in sclerophyllous forest (two species). No species of rodent was found to occur across the complete elevational range of the survey. *Eliurus minor* and *Rattus rattus* were found between 810 and 1875 m. One species was restricted to the lowland forest (*Eliurus webbi*) and another to the sclerophyllous forest (*Monticolomys koopmani*). In drier forests of parcel 2 and 3 the indigenous rodents showed low levels of diversity and density. Over the 20 km between the western side of parcel 1 and the eastern side of parcel 2 there is a complete turnover in native rodent species.

Résumé

Entre fin Octobre et fin Décembre 1995, une étude a été entreprise sur les rongeurs se trouvant à l'intérieur des trois Parcelles boisées qui forment la Réserve Naturelle Intégrale d'Andohahela. Au niveau de la Parcelle 1, composée d'une forêt humide, cinq zones d'altitudes comprises entre 440 m et 1875 m ont été étudiées. On a relevé sept espèces de rongeurs appartenant à la sous-famille endémique Nesomyinae (*Eliurus majori*, *E. minor*, *E. tanala*, *E. webbi*, *Gymnuromys roberti*, *Monticolomys koopmani*, et *Nesomys rufus*), ainsi qu'un membre d'une sous-famille introduite Murinae (*Rattus rattus*). Au niveau de la Parcelle 2, comprenant des broussailles épineuses et sèches et une forêt galerie humide, une Nesomyinae (*Eliurus myoxinus*) et *Rattus rattus* ont été relevées. Des rongeurs attrapés par des pièges dans la Parcelle 3, où on trouve un type de forêt intermédiaire entre les parties humides de la Parcelle 1 et les

¹Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, IL 60605-2496, U.S.A.

²Division of Mammals, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A.

³Route de St. Cergue, 1270 Trélex, Switzerland.

zones sèches de la Parcelle 2, comprennent *Eliurus myoxinus* et les deux espèces introduites Murinae *Rattus norvegicus* et *R. rattus*.

La diversité la plus importante des rongeurs indigènes dans la Parcelle 1 a été rencontrée à une altitude de 1200 m dans la forêt de montagne (cinq espèces), et la diversité la plus faible se trouve à une altitude de 400 m dans la forêt des zones basses (une espèce) et également à une altitude de 1875 m dans la forêt sclérophylle (2 espèces). On n'a trouvé aucune espèce commune de rongeur à travers la totalité de la région étudiée d'altitudes différentes. On a rencontré *Eliurus minor* et *Rattus rattus* à des altitudes comprises entre 810 m et 1875 m. Une espèce est limitée aux forêts des zones de basse altitude (*Eliurus webbi*) et une autre aux forêts sclérophylles (*Monticolomys koopmani*). Dans les forêts plus sèches des Parcelles 2 et 3, les rongeurs indigènes enregistrent des faibles niveaux de diversité et de densité. Sur les 20 km entre la limite à l'Ouest de la Parcelle 1 et la limite à l'Est de la Parcelle 2, on remarque une apparition totalement composée d'espèces de rongeurs indigènes.

Introduction

As the number of studies on the small mammals of Madagascar has increased over the past decade, taxonomic and distributional knowledge of the island's endemic rodents, subfamily Nesomyinae, has expanded accordingly (Carleton, 1994; Carleton & Goodman, 1996, 1998; Goodman & Carleton, 1996, 1998; Goodman et al., 1996a; Stephenson 1993, 1994, 1995). Several studies have looked at species turnover along elevational transects and now information is available from a variety of key sites in eastern humid forest, each set within a different mountain system (Fig. 14-1): Parc National (PN) de la Montagne d'Ambre, at 12.5°S (Raxworthy & Nussbaum, 1994; Goodman et al., 1996a, 1997a); Réserve Spéciale (RS) d'Anjanaharibe-Sud, at 14°S (Carleton & Goodman, 1998; Goodman & Carleton, 1998); and the Réserve Naturelle Intégrale (RNI) d'Andringitra at 22°S (Carleton & Goodman, 1996; Goodman & Carleton, 1996; Langrand & Goodman, 1997). Together with data available for other eastern reserves (e.g., PN de Ranomafana and RS d'Analamazaotra), information on nesomyine rodent diversity now covers much of the eastern humid forest, a long but narrow biome that once spanned most of Madagascar's rugged eastern versant. A notable omission to this geographical coverage involves those mountains and forests in extreme southeastern Madagascar. The 1995 biological inventory of the RNI d'Andohahela, a protected area including the southern part of the Anosyenne Mountains, redresses this regional void and advances systematic understanding of the native rodent fauna.

Much of the striking habitat diversity of Madagascar is concentrated in the island's southeast-

ern corner, where an abrupt ecotone demarcates wet and dry environments (Goodman et al., 1997b). The ecological contrast is largely influenced by the north-south alignment of the Anosyenne Mountains, which act as a rain barrier for weather systems moving in an east to west direction from the Indian Ocean (Battistini, 1964). Diminished precipitation associated with this rain shadow dramatically affects floristic structure and composition across this narrow zone, with changes evident over a distance of just a few kilometers. Thus, on the eastern or windward slopes of the Anosyenne Mountains, Madagascar's eastern humid forests reach their southern limits; although south of the Tropic of Capricorn, the humid forests are typically tropical in structure and species composition (White, 1983; see also Chapters 2 and 4 herein). From a few exposed ridges just kilometers to the west, on the leeward side of this range, one can view dry forest (spiny bush) with its characteristic baobab (*Adansonia*) trees and thick stands of cactus-like Didiereaceae. The nearby coastal plain retains stands of evergreen littoral forest, a once widespread woodland formation; such remnants have low canopies relative to lowland humid forest and rest on sandy, organically poor soils. The forests of southeastern Madagascar become progressively drier from north to south and abruptly so from east to west, changing to deciduous thicket and bush.

The RNI d'Andohahela is composed of three disjunct parcels that are separated by a minimum distance of 20 km (Fig. 14-2). Each parcel contains one or more distinct forest types: parcel 1—eastern humid forest, including lowland forest to high mountain sclerophyllous forest; parcel 2—spiny forest, with remnants of riverine gallery forest; and parcel 3—transitional forest, containing a

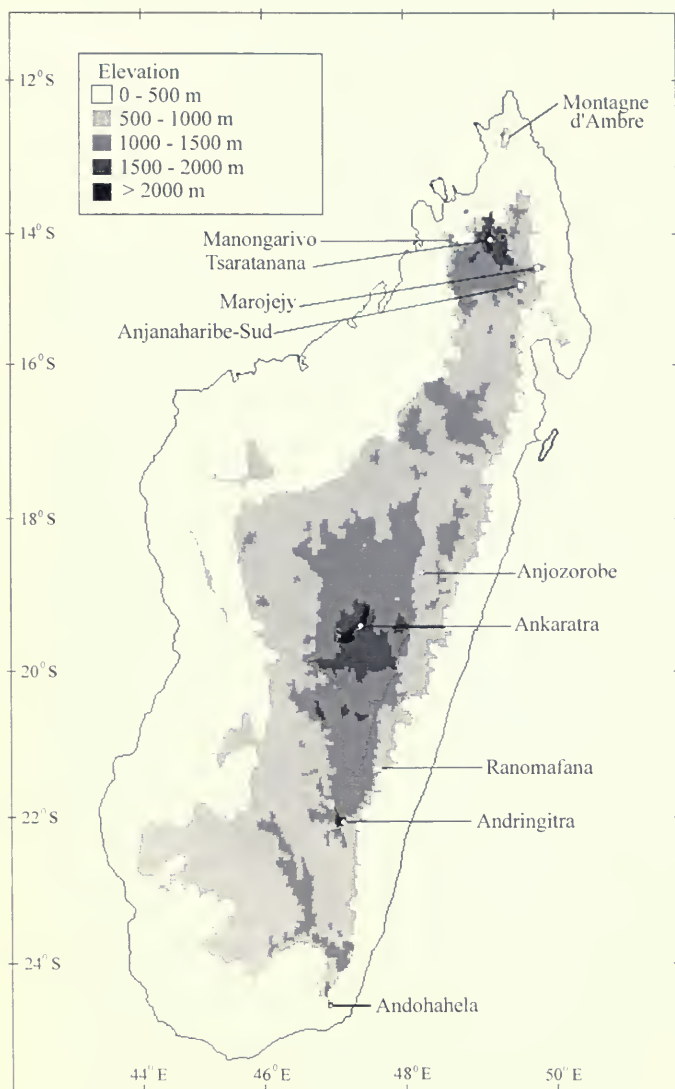


FIG. 14-1. Topography of Madagascar, illustrating places mentioned in the text, most of which have been surveyed for rodents. Note the relative isolation of the northern highlands, especially Montagne d'Ambre, the extensive area occupied by the Central High Plateau, and the extreme position of the RNI d'Andohahela near the terminus of the southern highlands.

mixture of elements from humid and dry forests (see Chapters 2 and 4 for detailed floristic descriptions of parcels 1 and 2). During the 1995 inventory an elevational transect was conducted at five stations (440–1875 m) in parcel 1, and single sites were sampled in parcels 2 (120 m) and 3 (170 m). This study presents the results of those surveys, documents the rodent diversity of the RNI d'Andohahela, and summarizes attendant natural history and biogeographic information. In addition, data on the nesomyine rodent community

within the RNI d'Andohahela are integrated with those now available from comparable inventories, which collectively embrace a broad expanse throughout Madagascar's great eastern forest from approximately 12.5° to 24.5° south latitude.

Previous Work in the Region

Between 1929 and 1931, the Mission Zoologique Franco-Anglo-Américaine (MZFAA) con-

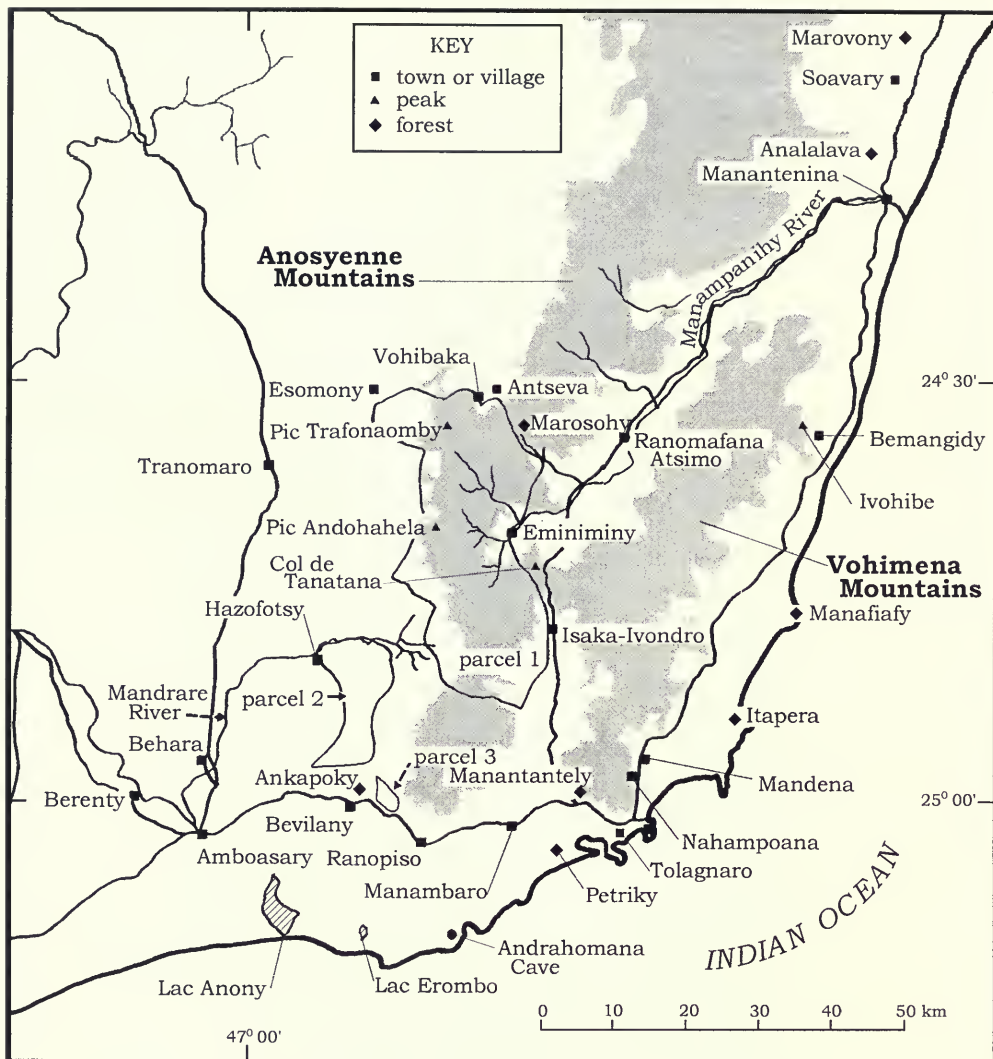


FIG. 14-2. Southeastern Madagascar, illustrating the three parcels of the RNI d'Andohahela, mountain ranges, and other local place names and geographical features referenced in the text. Areas shaded in gray denote elevations above 700 m and emphasize the principally north-south orientation of the Anosyenne and Vohimena mountains.

ducted the most ambitious geographical survey of Malagasy birds and mammals to date, but the itinerary of this group of scientists did not include the extreme southeastern corner of the island. One field team visited a forest 20 km west of Vondrozo (Rand, 1936), the MZFAA site closest to the RNI d'Andohahela but a distant 200 km north of parcel 1, and coastal plain near Manombo, just to the south of Farafangana. Rodents collected at these places include *Eliurus minor*, *E. webbi*, *Gymnomys roberti*, and *Nesomys audeberti*, vouchers of which are preserved in the American Museum of Natural History (AMNH; New York), the Brit-

ish Museum of Natural History (BMNH; London; now The Natural History Museum), or the Muséum National d'Histoire Naturelle (MNHN; Paris).

In 1944, Cecil S. Webb, a resourceful naturalist and collector sponsored by the BMNH, visited a few areas to the west of Tolagnaro, where he obtained small mammals, particularly rodents (Carleton & Schmidt, 1990). He worked two localities in the vicinity of the RNI d'Andohahela: 5 mi (8.0 km) E of Bevilany, which is just southwest of parcel 3; and 7 mi (11.3 km) NE of Lac Anony, near the coast and farther to the southwest

of the reserve (Fig. 14-2). The rodents collected consist of *Eliurus myoxinus* and *Macrotarsomys bastardi*, specimens of which are deposited in BMNH.

As part of a study of mammals and their role as disease vectors, Harry Hoogstraal visited several places in southeastern Madagascar in December 1948 (Hoogstraal 1953; Uilenberg et al., 1979). His stops included Mandena and the forest of Bemangidy (approximately 72 km north of Tolagnaro), along the eastern slope of the Vohimena Mountains (Fig. 14-2). Hoogstraal made a small general collection of open country and forest-dwelling mammals that is housed in the Field Museum of Natural History (FMNH; Chicago) and the National Museum of Natural History (USNM; Washington, D.C.); among them is a single specimen of *Nesomys audeberti* taken in original forest near Bemangidy. On the basis of two reconnaissance trips in 1989 and 1990, S.M.G. found that the area still contains relatively undisturbed humid forest, particularly on the slopes below Pic Ivohibe.

In 1989 and 1990, a field team was assembled to assess the potential biological impact of a proposed mining project in southeastern Madagascar. This faunal inventory is referred to as the QIT-FER project, and G. Ken Creighton coordinated the small mammal studies in collaboration with E. Raholimavo, D. Rakotondravony, and J. Ryan. Numerous localities, containing a variety of habitat types, were visited, but emphasis was devoted to the humid littoral forests of Mandena and Manafiafy, north of Tolagnaro, and to the dry littoral forest of Petriky, west of Tolagnaro (Fig. 14-2). These three sites are adjacent to or part of the proposed mining sites, but the QIT-FER team surveyed other places in their vicinity in order to provide a regional faunal perspective. Two lowland humid forests in the Vohimena Mountains and near Tolagnaro were surveyed; the elevational sampling at both of these sites ranged from 100 to 450 m, including the Manantantely Forest at the southern end of the chain and the Nahampoana Forest on the eastern slopes. To augment information on elevational variation, the humid forest of Marosohy, along the northeastern boundary trail of parcel 1 of the RNI d'Andohahela, was studied at 425 and 725 m. Finally, they visited the spiny bush forest of Ankapoky, just south of parcel 2 and west of parcel 3 of the RNI d'Andohahela; this site is very close to Webb's old locality at 5 mi E of Bevilany (Fig. 14-2). Specimens collected during this survey are depos-

ited in the Département de Biologie Animale, Université d'Antananarivo, Antananarivo (UAD-BA), and the USNM.

We have examined the nesomyine rodents collected during these several field studies and have generally referenced them to augment the taxonomic and distributional context of material procured during the 1995 survey of the RNI d'Andohahela.

Materials and Methods

This study is based on fieldwork conducted between 19 October and 29 December 1995 by S.M.G. and M.P. Taxonomic determinations were verified by M.D.C., who also undertook systematic comparisons.

Field Methods and Trapping Protocol

The general field protocols follow those previously outlined in parallel reports on the rodents of the RNI d'Andringitra (Goodman & Carleton, 1996) and the RS d'Anjanaharibe-Sud (Goodman & Carleton, 1998). Information is presented on the rodent faunas of all three parcels within the RNI d'Andohahela. Five altitudinal zones (440, 810, 1200, 1500, and 1875 m) were studied within the humid forest of the reserve (parcel 1). The areas surveyed at 440 and 810 m showed signs of both ancient and recent human disturbance, whereas the other three sites were in seemingly undisturbed habitat. Immediately after termination of the elevational transect in parcel 1, the survey group moved to the spiny bush area of the reserve (parcel 2) and trapped one site in disturbed habitat at 120 m. For all sites visited in parcels 1 and 2, trap lines were maintained for a minimum of 7 nights (Table 14-1). Each trap line, numbered sequentially starting with the 440 m zone, consisted of Sherman live traps ($9 \times 3.5 \times 3$ in.) and National live traps ($16 \times 5 \times 5$ in.), at a ratio of 4:1. Traps were baited daily, generally between 1500 and 1700 hr, with finely ground peanut butter; lines were visited and traps inspected at least twice daily, once at dawn and again in late afternoon. At each of these sites, sampling was also conducted with pitfall traps, but this technique yielded few rodents (see Chapter 13). In late December 1995, M.P. visited the transitional forest of parcel 3 and trapped for 5 nights at 170 m.

TABLE 14-1. Summary of trap lines in the RNI d'Andohahela.*

Elevation	No. of traps	Length (m) of line	Mean distance (m) between traps	Mean height (m) above ground
Parcel 1				
440 m (20–27 Oct)				
Line 1	85	894	7.7 \pm 6.42 (1–38)	1.4 \pm 0.65 (0.2–2.5), n = 30 (35%)
Line 2	50	490	9.5 \pm 3.50 (3–21)	1.5 \pm 0.76 (0.3–3.0), n = 17 (34%)
810 m (29 Oct–5 Nov)				
Line 3	50	548	10.3 \pm 3.75 (1–22)	1.8 \pm 0.73 (0.2–3), n = 21 (42%)
Line 4	75	510	7.5 \pm 4.66 (0.5–21)	1.4 \pm 0.59 (0.3–3), n = 28 (37%)
1200 m (8–16 Nov)				
Line 5	50	373	7.6 \pm 2.81 (4–17)	1.8 \pm 0.82 (0.2–3), n = 23 (46%)
Line 6	75	364	4.9 \pm 3.11 (1–18)	1.6 \pm 0.46 (0.5–3), n = 27 (36%)
1500 m (17–26 Nov)				
Line 7	50	375	7.5 \pm 3.51 (0.5–17)	1.8 \pm 1.13 (0.1–4), n = 18 (36%)
Line 8	75	454	6.1 \pm 3.63 (1–17)	2.0 \pm 0.46 (1.5–3), n = 17 (23%)
1875 m (27 Nov–4 Dec)				
Line 9	50	255	6.3 \pm 3.12 (0.5–14)	1.9 \pm 0.53 (1–2.8), n = 31 (62%)
Line 10	75	415	5.6 \pm 3.48 (1–13)	1.7 \pm 0.62 (0.5–3), n = 28 (37%)
Parcel 2				
120 m (8–14 Dec)				
Line 11	50	553	11.1 \pm 5.18 (2–21)	1.9 \pm 0.47 (0.2–2.4), n = 22 (44%)
Line 12	75	760	10.1 \pm 4.31 (1–19)	1.8 \pm 0.62 (0.5–2.5), n = 27 (36%)

* Each line consisted of National and Sherman live traps in a ratio of 4:1 (see page 221).

Descriptive statistics are presented as the mean \pm standard deviation, with the range in parentheses.

This visit was intended only to assess what rodents commonly occurred in this forest type, not to comprehensively document species diversity as for other sites visited within this reserve.

A trap-night is defined as one live trap in use for a 24 hr period (dawn to dawn). The total number of trap-nights accrued in each elevation varied slightly; consequently, the first 500 trap-nights in an elevational zone are considered the "standardized" trapping regimen in order to facilitate comparisons among the sites sampled. Standing biomass of a species is based on the total catch of individuals during a standardized trapping regimen multiplied by the average body weight of the species (Table 14-2). We depended exclusively on live trap techniques during this inventory for reasons explained previously (Goodman & Carleton, 1998, p. 201).

To quantify differences in the spatial distribution of small mammal captures, several trapping variables were systematically recorded for each trap installed: (1) type of trap; (2) total length of trap line; (3) distance between traps; and (4) specific placement of trap, including its substrate, surrounding forest structure, and position on or height above the ground. Categorization of microhabitat was simplified from a more detailed sys-

tem used earlier (Goodman & Carleton, 1996), as follows:

ON GROUND—(1) In leaf litter, generally in area of open understory; (2) under decomposed downed trees or woody vegetation; (3) by tree root or trunk, with or without cavity or hole; or (4) miscellaneous, including placement under exposed rocks or boulders, at base of rock face, at entrance of hole in ground, in thick herbaceous vegetation, or on moss-covered rocks.

ABOVE GROUND—(1') On liana, limb, or trunk of <10 cm diameter in horizontal to vertical position; (2') on liana, limb, or trunk of >10 cm diameter in horizontal to vertical position; (3') on limbs or trunks suspended by lianas; or (4') miscellaneous, including placement on bamboo stalks, in small cavities at junctions of tree limbs, or on large moss-covered rocks.

Specimens and Measurements

Captured animals were prepared as standard museum skins with associated skulls and partial skeletons, as fluid-preserved carcasses, or as full skeletons. Whole carcasses were wrapped in fine cheesecloth before immersion in formalin to pre-

TABLE 14-2. External measurements and sample statistics for adult rodents collected in the RNI d'Andohahela.

Species	TOTL	HBL	TL	HFL	EL	WT
<i>Rattus norvegicus</i>	322	157	154	32	23	96
<i>Rattus rattus</i>	393.5 10.3 370-405 (n = 10)	168.3 8.5 160-181 (n = 8)	206.6 8.6 190-216 (n = 10)	34.1 2.0 32-39 (n = 10)	25.1 1.4 23-28 (n = 10)	144.6 7.4 132-155 (n = 10)
<i>Eliurus majori</i>	354, 358	155.2 8.5 145-168 (n = 5)	189, 190	30.2 1.6 29-33 (n = 5)	22.4 2.4 20-25 (n = 5)	99.6 11.5 86.5-113 (n = 5)
<i>Eliurus minor</i>	239.8 7.2 230-254 (n = 15)	106.5 4.1 99-113 (n = 22)	128.0 5.5 115-137 (n = 15)	21.8 0.7 21-23 (n = 22)	18.8 1.4 15-21 (n = 22)	38.5 4.4 31.0-47.0 (n = 22)
<i>Eliurus myoxinus</i>	283.7 37.8 251-325 (n = 3)	130.0 14.8 120-147 (n = 3)	147.7 23.1 126-172 (n = 3)	27.7 1.5 26-29 (n = 3)	22.7 0.6 22-23 (n = 3)	65.8 19.7 48.0-87.0 (n = 3)
<i>Eliurus tanala</i>	339.5 14.8 303-362 (n = 15)	149.3 5.5 131-159 (n = 18)	181.7 11.1 152-197 (n = 16)	30.5 1.4 28-34 (n = 20)	23.6 1.3 21-25 (n = 19)	94.3 13.7 76.5-134 (n = 20)
<i>Eliurus webbi</i>	331.4 12.7 309-347 (n = 12)	146.1 5.3 134-154 (n = 18)	175.0 11.7 154-191 (n = 12)	30.2 0.9 29-32 (n = 18)	23.3 1.2 21-25 (n = 17)	88.3 6.6 77.0-99.5 (n = 18)
<i>Gymnuromys roberti</i>	360	157	184	37	23	120
<i>Monticolomys koopmani</i>	227.4 7.2 217-236 (n = 5)	86.2 1.9 84-89 (n = 5)	134.4 5.9 127-142 (n = 5)	23.6 0.6 23-24 (n = 5)	18.8 0.8 18-20 (n = 5)	22.6 3.8 18.5-27.5 (n = 5)
<i>Nesomys rufus</i>	364.0 16.5 345-375 (n = 3)	184.0 7.5 177-191 (n = 4)	169.7 11.0 159-181 (n = 3)	44.3 1.0 43-45 (n = 4)	26.3 1.0 25-27 (n = 4)	182.0 12.7 164-191 (n = 4)

Abbreviations are explained in the Materials and Methods section. The sample statistics are given as the mean, standard deviation, and range, with the number of animals in parentheses.

vent loss or mixing of ectoparasites between their specific hosts. A large proportion of the captured rodents during our work in the RNI d'Andohahela were prepared as vouchers. This material is housed in the FMNH, and a representative series has been returned to the UADBA. Specimens deposited immediately after the survey in the latter institution have not yet been catalogued and are individually referenced by the collector's field numbers (UA-SMG or UA-MP). To confirm taxonomic identifications, nesomyine holdings in other museums (see Appendix 22-1, p. 283, in Goodman & Carleton, 1996) were also consulted, including the holotypes of all described forms of Nesomyinae except Peters' (1870) *Nesomys rufus*.

Six measurements, in millimeters (mm) or grams (g), were taken by S.M.G. for each specimen in the flesh. Measurement abbreviations and definitions are given below.

- TOTL (total length of body and tail): from the tip of the nose to the end of the last caudal vertebra (not including terminal hair tuft)
- HBL (head and body length): from the tip of the nose to the distalmost point of the body (at base of tail)
- TL (tail length): from the base of the tail (held at right angles to the body) to the end of the last caudal vertebra (not including terminal hair tuft)

HFL (hind foot length): from the heel to the tip of the longest toe (not including claw)
 EL (ear length): from the basal notch to the distal tip of the pinna
 WT (weight): measured with Pesola spring scales, to ± 0.5 g for animals < 100 g and to ± 1.0 g for those between 101 and 300 g.

Sixteen cranial and two dental dimensions were measured by M.D.C. to the nearest 0.1 mm using handheld digital calipers accurate to 0.03 mm. These measurements, and their abbreviations, follow the anatomical landmarks defined and illustrated previously (Carleton, 1994).

BBC, breadth of the braincase
 BIF, breadth of incisive foramina
 BM1s, breadth of the bony palate across the first upper molars
 BOC, breadth across the occipital condyles
 BR, breadth of rostrum
 BZP, breadth of the zygomatic plate
 DAB, depth of the auditory bulla
 IOB, interorbital breadth
 LBP, length of bony palate
 LD, length of diastema
 LIF, length of the incisive foramina
 LM1-3, coronal length of maxillary toothrow
 LR, length of rostrum
 ONL, occipitonasal length
 PPB, posterior breadth of the bony palate
 PPL, postpalatal length
 WM1, width of the first upper molar
 ZB, zygomatic breadth

Standard descriptive statistics (mean, range, standard deviation) were derived for adult specimens in each species sample. We define "adult" as the age cohort consisting of animals that lack the finer, juvenile pelage and possess fully erupted, though sometimes unworn, third molars. Where sample sizes permitted, two-sample *t*-tests and one-way analyses of variance were applied to the mensural variables, with sex as the categorical variable. Analytical routines were carried out using Systat (version 6.01, 1996). The mammae formula is presented as the number of paired postaxial, abdominal, or inguinal teats.

To assess faunal similarities among geographic regions, we used the Jaccard Index, a matching coefficient that scales similarity to range from 0 to 1:

$$\text{Jaccard Index} = \frac{N_c}{N_1 + N_2 - N_c}, \quad (1)$$

where N_1 = the number of species at site 1 (the smaller fauna), N_2 = the number of species at site 2, and N_c = the number of species common to both sites. The indices from these pairwise comparisons were clustered using UPGMA as implemented by Systat.

Accounts of Species

Information on the natural history and elevational range of each rodent species captured during the survey of the RNI d'Andohahela is presented under the subheadings DISTRIBUTION, ECOLOGY AND REPRODUCTION, COMMENTS (when necessary), and SPECIMENS EXAMINED. The last subheading includes only material collected in the reserve during the 1995 mission. More detailed criteria for species identification and discussion of alpha-level taxonomic problems are presented in Carleton (1994), Carleton and Goodman (1996, 1998), and Goodman and Carleton (1996, 1998). External measurements and masses are given here for the rodent species captured during the 1995 survey to aid researchers in identification of Malagasy rodents and to provide baseline data for some of the analyses presented in the Discussion section.

Family Muridae: Subfamily Murinae

Rattus norvegicus (Berkenhout, 1769)

DISTRIBUTION—This introduced species was trapped only within parcel 3. A single individual taken near the main road between Tolagnaro and Amboasary-Sud was obtained in a line that yielded several specimens of *Rattus rattus* and *Eliurus myoxinus*. In general, *R. norvegicus* is a commensal species that is particularly common in urban centers and rural communities, and notably uncommon in agricultural fields and at the forest edge (Malzy, 1964; Rakotondravony, 1992).

ECOLOGY AND REPRODUCTION—The single individual, an adult female with small mammae and a perforated vagina, entered a trap set on a 5-cm-diameter branch (2.2 m above ground) of a large emergent tree.

TABLE 14-3. Trap success for *Rattus rattus* in the humid forest of parcel 1 of the RNI d'Andohahela.

Elevation (m)	Number captured	Number of trap-nights	Capture rate per 100 trap-nights
440	0	845	0.0
810	4	850	0.47
1200	0	775	0.0
1500	5	1,050	0.48
1875	2	875	0.23

SPECIMENS EXAMINED—Parcel 3, 6 km SE of Bevilany, 25°01.3'S, 46°38.8'E, 170 m (FMNH 156536).

Rattus rattus (Linnaeus, 1758)

DISTRIBUTION—*Rattus rattus* occurs in all three parcels of the RNI d'Andohahela. This introduced species is known from a variety of habitats on the island, including pristine forest (Stephenson, 1993; Goodman, 1995; Goodman & Carleton, 1996, 1998).

ECOLOGY AND REPRODUCTION—Previous work along elevational transects in the eastern humid forest indicated that *Rattus rattus* is more common at mid-elevations than in lowland forest or near the summit (Goodman et al., 1997a; Goodman & Carleton, 1996, 1998). This pattern did not hold within the RNI d'Andohahela, where no marked change was recorded in the density of this species when present, as measured by trap success, along the elevational gradient (Table 14-3). During the period of our field study, *R. rattus* was encountered less frequently in the RNI d'Andohahela than on other mountains with similar botanical communities and altitudinal stratification. For example, at 1350 m on Montagne d'Ambre, *R. rattus* was ubiquitous, totaling 85% of all trap captures (Goodman et al., 1997a); in the same highland zone of the RNI d'Andohahela, none were captured at 1200 m, and only five individuals were trapped in 1,050 trap-nights at 1500 m (Table 14-3). Like its altitudinal pattern on those other mountains, however, *R. rattus* was found to occur in the deep forest of parcel 1 but was not trapped at the lowest elevational zone closest to the forest edge. Populations of the species appear to be most abundant in the zone between 1500 and 1625 m, as judged from trap captures in the RNI d'Andohahela, RNI d'Andringitra, and RS d'Anjanaharibe-Sud (Table 14-3; Goodman & Carleton, 1996, 1998).

In the dry deciduous Kirindy Forest, near Morondava, *R. rattus* is rare in the large relatively intact forest block (Ganzhorn et al., 1996). This rat is common in small satellite forests, however, and its presence is significantly and negatively associated with the occurrence of the nesomyines *Eliurus myoxinus* and *Macrotarsomys bastardi*. This explanation fits our observations of the dry forests sampled in the RNI d'Andohahela. In parcel 2 the single *R. rattus* taken in 1,023 trap-nights inhabited disturbed gallery forest along a small river, and in parcel 3 all individuals captured were in close proximity to a stream. Earlier trapping (144 trap-nights using Sherman traps baited with banana) in parcel 3 conducted in late January 1990 yielded three *E. myoxinus* and no *Rattus* (Pidgeon, unpubl. data).

Of the 11 *R. rattus* captured within parcel 1 and for which there is information on trap placement, all except one were taken on the ground (Table 14-4). The majority of trap sets were placed near streambeds, rocky outcrops, or at the base of large trees with buttressed roots. The single arboreal capture involved a trap placed on an 8-cm-diameter tree trunk (2.5 m above ground) leaning at 30° into a liana tangle.

Twelve specimens of *R. rattus* were examined for reproductive condition: six males with scrotal testes, two males with abdominal testes, three adult females with mammae enlarged or actively lactating, and one subadult female. The mammae formulae varied from 1-1-2 (n = 1) to 1-2-2 (n = 2).

COMMENTS—*Rattus rattus* constitutes a substantial portion of prey taken by *Asio madagascariensis* in southeastern Madagascar. At a roost in the Nahampoana Forest, within the ecotone between lowland humid forest and an agricultural area, about 40% of the prey consumed by this owl is *R. rattus* (Goodman et al., 1993).

Southeastern Madagascar has been settled and occupied by humans since at least the 9th century (Wright & Rakotoarisoa, 1997). Tolagnaro (Fort Dauphin) has been a major port of international shipping since the 16th century, allowing more than 400 years for colonization of the region by seagoing *Rattus*. Etienne de Flacourt, a representative of the French *Compagnie des Indes Orientales*, based at Fort Dauphin in the latter half of the 17th century, noted (1658) that rats and mice were common everywhere and caused considerable destruction of grain in houses and agricultural fields. Areas in and around parcel 1 of the RNI d'Andohahela have witnessed human pres-

TABLE 14-4. Microhabitat occurrences of rodent species by elevation in parcel 1 of the RNI d'Andohahela.

Elevation and species	No. taken	Trap position		Ground location*				Aboveground location			
				Leaf litter	Under rotten wood	By roots, trunks	Misc.	Vine, limb, or trunk <10 cm	Limbs, trunks >10 cm	Sus- pended trunks	Misc.
440 m											
Trap distribution		88	47	20	15	26	27	25	15	3	4
<i>Eliurus webbi</i>	13						1	5	6		1
810 m											
Trap distribution		76	49	21	5	17	33	26	15	1	7
<i>Rattus rattus</i>	4						3	1			
<i>Eliurus minor</i>	2							2			
<i>Eliurus tanala</i>	8			1			2	3	2		
<i>Eliurus webbi</i>	6			1		1	1		3		
<i>Nesomys rufus</i>	1			1							
1200 m											
Trap distribution		74	51	17	4	31	22	21	20	5	5
<i>Eliurus majori</i>	2						1			1	
<i>Eliurus minor</i>	9					1		2	3	3	
<i>Eliurus tanala</i>	5					3			2		
<i>Gymnuromys roberti</i>	1						1				
<i>Nesomys rufus</i>	2				1		1				
1500 m											
Trap distribution		81	44	8	17	30	26	13	25	0	6
<i>Rattus rattus</i>	5			2			3				
<i>Eliurus majori</i>	4						1	2	1		
<i>Eliurus minor</i>	7				1			3	3		
<i>Eliurus tanala</i>	11			1	1	2	5		2		
1875 m											
Trap distribution		64	61	15	3	19	27	17	41	2	1
<i>Rattus rattus</i>	2					1	1				
<i>Eliurus minor</i>	3					2	1				
<i>Monticolomys koopmani</i>	5			4			1				
Totals: 440–1875 m											
Trap distribution		383	252	81	44	123	135	102	116	11	23
<i>Rattus rattus</i>	11	10	1	2		1	7	1			
<i>Eliurus majori</i>	6	2	4				2	2	1	1	
<i>Eliurus minor</i>	21	5	16		1	3	1	7	6	3	
<i>Eliurus tanala</i>	26	15	11	2	1	5	7	4	7		
<i>Eliurus webbi</i>	19	4	15	1		1	2	5	9		1
<i>Gymnuromys roberti</i>	1	1					1				
<i>Monticolomys koopmani</i>	5	5		4			1				
<i>Nesomys rufus</i>	3	3		1	1		1				
Total captured	92	45	47	10	3	10	22	19	23	4	1

* See p. 222 for habitat definitions.

ence since the 15th or 16th centuries (Razanababiny, 1995; Goodman & Rakotoarisoa, 1998; Rakotoarisoa, 1998). Thus, even given the long-term presence of *Rattus* in the region, the species has not yet exploited humid forest habitats en masse, as it has some other areas of the island

(Goodman et al., 1997a). The factors influencing this colonizing variation are unknown and warrant detailed examination, particularly in view of the likelihood that *R. rattus* may be displacing certain endemic rodents in some regions (Goodman, 1995; Ganzhorn et al., 1996).

SPECIMENS EXAMINED—Parcel 1, 12.5 km NW of Eminiminy, 24°35.6'S, 46°44.3'E, 810 m (FMNH 156537; UA-MP 21; UA-SMG 7475, 7483); parcel 1, 15.0 km NW of Eminiminy, 24°34.2'S, 46°43.9'E, 1500 m (FMNH 156538–156540, 156544, 156582); parcel 1, 20.0 km SE of Andranondambo, 24°33.7'S, 46°43.3'E, 1875 m (FMNH 156541); parcel 2, 7.5 km ENE of Hazofotsy, 24°49.0'S, 46°36.6'E, 120 m (FMNH 156543); parcel 3, 6 km SE of Bevilany, 25°01.3'S, 46°38.8'E, 170 m (FMNH 156545–156548).

Family Muridae: Subfamily Nesomyinae

Eliurus majori Thomas, 1895

DISTRIBUTION—Specimens from the RNI d'Andohahela extend the range of *Eliurus majori* 260 km further south of its previously known limit in the RNI d'Andringitra (Carleton, 1994; Goodman & Carleton, 1996). This rodent is now known to occur in wet forest on numerous mountains along the length of the island, from PN de la Montagne d'Ambre in the north, through RS d'Anjanaharibe-Sud, Anjozorobe, Ambohimantambo, and RNI d'Andringitra, to RNI d'Andohahela in the south (Fig. 14-1; Carleton, 1994; Goodman & Carleton, 1996, 1998; Goodman et al., 1996a; Goodman et al., 1998). Its occurrence in the Anosyenne Mountains, at 1200 and 1500 m of parcel 1, conforms to the general altitudinal setting documented elsewhere—a belt of middle to upper montane forest from 1000 to 2000 m (Goodman & Carleton, 1996, 1998).

ECOLOGY AND REPRODUCTION—Four of five *E. majori* were captured in a variety of arboreal placements (Table 14-4), a result similar to that reported for the species in the RNI d'Andringitra and RS d'Anjanaharibe-Sud. In the RNI d'Andohahela, successful trap sets included relatively thin branches and lianas of <10 cm diameter, a large branch of 25 cm diameter, and a section of a fallen tree trunk suspended in a vine tangle. Two animals were obtained in traps placed on the ground, both at the base of large boulders or rocky outcrops that sheltered holes and hollows.

Of the five individuals captured, three are adult males with large scrotal testes and convoluted epididymides, and two are adult females with prominent mammae. One female has three placental scars. The mammae total six ($n = 2$), distributed

as one pair postaxial, one pair abdominal, and one pair inguinal, a formula consistent with individuals from the RS d'Anjanaharibe-Sud and with the genus (Carleton, 1994; Goodman & Carleton, 1998).

SPECIMENS EXAMINED—Parcel 1, 13.5 km NW of Eminiminy, 24°35.0'S, 46°44.1'E, 1200 m (FMNH 156503, 156615); parcel 1, 15.0 km NW of Eminiminy, 24°34.2'S, 46°43.9'E, 1500 m (FMNH 156616, 156617, 156658).

Eliurus minor Major, 1896a

DISTRIBUTION—The 1995 inventory found *Eliurus minor* to occur broadly in forest between 810 and 1875 m (Table 14-5). This elevational range resembles the distribution in the RNI d'Andringitra, where the species was recorded from 720 to 1625 m (Goodman & Carleton, 1996). Carleton (1994) reported the presence of *E. minor* at 20 km west of Vondrozo (500 m), a MZFAA locality visited in 1929 (Rand, 1932). More recently, the species was collected by the QIT team in the Marosohy Forest between 350 and 450 m, a place near the northeastern boundary trail of parcel 1, RNI d'Andohahela. *Eliurus minor* is now known throughout the eastern humid forest, from Montagne d'Ambre in the north to the RNI d'Andohahela in the south (Carleton, 1994; Goodman et al., 1996a).

ECOLOGY AND REPRODUCTION—Of 21 *E. minor* obtained in traps, 16 (76%) were taken in arboreal sets, of which seven were on vines and branches of <10 cm diameter (Table 14-4). The five *E. minor* caught in ground traps were in a variety of situations, such as next to tree root buttresses, at the opening of a tunnel system in the soil adjacent to a dead and hollow tree, at the base of rotten and fallen tree trunks, and in relatively open understory dominated by a herbaceous growth of Acanthaceae. Furthermore, two *E. minor* were obtained in pitfall traps (see Chapter 13). On the basis of trap captures along small branches and vines as well as terrestrial sets, this species appears to be predominantly scansorial.

Most individuals of *E. minor* trapped in the 810, 1200, and 1500 m zones were adults (Table 14-6), and most showed signs of active breeding. Counts of embryos and placental scars of four females uniformly disclosed a litter size of three. No apparent synchrony was noted in the reproductive cycles of individuals captured within an elevational zone. Mammae counts for the nine fe-

TABLE 14-5. Elevational occurrence (m) of rodents within the three parcels of the RNI d'Andohahela based on the 1995 inventory.

Species	1*					2*	3*
	440	810	1200	1500	1875	120	170
Murinae							
<i>Rattus norvegicus</i>							+
<i>Rattus rattus</i>		+		+	+	+	+
Nesomyinae							
<i>Eliurus majori</i>			+	+			
<i>Eliurus minor</i>		+	+	+	+		
<i>Eliurus myoxinus</i>						+	+
<i>Eliurus tanala</i>		+	+	+			
<i>Eliurus webbi</i>	+	+					
<i>Gymnuromys roberti</i>			+				
<i>Monticolomys koopmani</i>					+		
<i>Nesomys rufus</i>		+	+				
Total species	1	5	5	4	3	2	3
Native species	1	4	5	3	2	1	1

* Parcel 1, humid forest ranging from lowland to sclerophyllous forest; parcel 2, spiny bush; parcel 3, transitional between humid forest and spiny bush. The floristic composition of these forest types is detailed in Chapter 2.

males for which information is available varied from 1-1-1 ($n = 2$) to 1-0-2 ($n = 6$) and 0-2-1 ($n = 1$).

COMMENTS—Remains of *Eliurus minor* have been identified in regurgitated pellets from *Asio madagascariensis* within the Nahampoana Forest north of Tolagnaro (Goodman et al., 1993). The site is at near the edge of lowland forest and encroaching agricultural fields.

SPECIMENS EXAMINED—Parcel 1, 12.5 km NW of Eminiminy, 24°35.6'S, 46°44.3'E, 810 m (FMNH 156618–156620); parcel 1, 13.5 km NW of Eminiminy, 24°35.0'S, 46°44.1'E, 1200 m (FMNH 156504, 156505, 156621–156624; UA-MP 23; UA-SMG 7523, 7551); parcel 1, 15.0 km NW of Eminiminy, 24°34.2'S, 46°43.9'E, 1500 m (FMNH 156506–156510, 156626, 156629, 156533; UA-MP 32); parcel 1, 20.0 km SE of Andranondambo, 24°33.7'S, 46°43.3'E, 1875 m (FMNH 156625, 156627, 156628).

Eliurus myoxinus Milne Edwards, 1885

DISTRIBUTION—*Eliurus myoxinus* is a widespread inhabitant of spiny bush and deciduous forest of western and southern Madagascar (Carleton, 1994; Goodman & Ganzhorn, 1994; Ganzhorn et al., 1996; Goodman & Rasoloarison, 1997). In the RNI d'Andohahela, this species is limited to the spiny bush forest of parcel 2 and

transitional forest of parcel 3. Webb had earlier collected *E. myoxinus* from the hills east of Bevilany, within 5–6 km of the southern boundary of parcel 2 (Carleton, 1994), and Creighton more recently obtained it in the Petriky Forest, 5–7 km SE of Manambaro, the easternmost limit so far known for the species.

ECOLOGY AND REPRODUCTION—All three *E. myoxinus* obtained during the 1995 mission were caught in arboreal trap sets, both on trunks and branches of >10 cm diameter (two specimens) and <10 cm diameter (one). Our findings underscore Webb's (1954) perception that the species is arboreal. In parcel 3 one animal was taken on a horizontal branch of a fruiting Apocynaceae tree next to a *Dypsis decaryi* (Arecaceae) palm tree endemic to parcel 3 and its immediate vicinity. It has been proposed that *Eliurus* consumes the fruits of this latter tree (J. Ratsirarson, pers. comm.).

With just three specimens captured, little can be said about the reproductive season of *E. myoxinus*. Two of the animals trapped are females, one with large and the other with small mammae; the third individual is an adult male with scrotal testes. The mammae formula is typical of *Eliurus*.

SPECIMENS EXAMINED—Parcel 2, 7.5 km ENE of Hazofotsy, 24°49.0'S, 46°36.6'E, 120 m (FMNH 156630); parcel 3, 6 km SE of Bevilany, 25°01.3'S, 46°38.8'E, 170 m (FMNH 156511, 156312).

TABLE 14-6. Age ratios and reproductive condition of rodents captured (standard live-traps) in parcel 1 of the RNI d'Andohahela.

Species	440 m		810 m		1200 m		1500 m		1875 m		440-1875 m		Individuals captured in reproductive state
	A/S	M/F	A/S	M/F	A/S	M/F	A/S	M/F	A/S	M/F	A/S	M/F	
<i>Rattus rattus</i>	—	—	4/2	4/0	—	—	5/0	2/3	1/1	1/0	10/3	7/3	77%
<i>Eliurus majori</i>	—	—	—	—	2/0	1/1	4/0	3/1	—	—	6/0	4/2	100%
<i>Eliurus minor</i>	—	—	5/1	1/4	6/1	4/2	7/1	5/3	0/1	0/0	18/4	10/9	86%
<i>Eliurus tanala</i>	—	—	4/4	3/1	4/1	4/1	6/5	2/4	—	—	14/10	9/6	63%
<i>Eliurus webbi</i>	5/9	2/3	7/1	3/4	—	—	—	—	—	—	12/10	5/7	55%
<i>Gymnureomys roberti</i>	—	—	—	—	1/0	0/1	—	—	—	—	1/0	0/1	100%
<i>Monticolomys koopmanni</i>	—	—	—	—	—	—	—	—	3/2	2/1	3/2	2/1	60%
<i>Nesomys rufus</i>	—	—	2/0	0/2	2/0	2/0	—	—	—	—	4/0	2/2	100%
Totals	5/9	2/3	22/8	11/11	15/2	11/5	22/6	12/11	4/4	3/1	68/29	39/31	72%
Individuals captured in reproductive state	36%		73%		94%		82%		50%		72%		

Abbreviations: A/S = numbers of adults and sub-adults; M/F = males with scrotal testes and females with large mammae, lactating, or carrying embryos. Not every specimen was examined for reproductive activity, so the tallies of individuals may be less than those presented for general trapping results (Table 14-8).

Eliurus tanala Major, 1896a

DISTRIBUTION—This species is widespread in the eastern humid forest, previously reported from the forest of Didy, near Lac Alaotra, as far south as the Vinanitelo region (Carleton, 1994). *Eliurus tanala* actually occurs further north than Didy; it was recently obtained between 875 and 1260 m in the RS d'Anjanaharibe-Sud (Goodman & Carleton, 1998). In the RNI d'Andohahela, *E. tanala* was recovered from pristine forest in parcel 1, between 810 and 1500 m (Table 14-5), but was not recorded from the dry lowland formations in parcels 2 and 3. The species was also collected during the QIT-FER studies in the Marosohy Forest (800 m) and Manantantely Forest (100-450 m). Together these localities in the Anosyenne Mountains and Vohimena Mountains extend the southern distributional limit of the species. This limit appears to coincide with the southernmost projection of middle montane forest in these highlands.

ECOLOGY AND REPRODUCTION—Eleven of 26 *E. tanala* obtained in trap lines involved sets above the ground, and 15 were on the ground (Table 14-4). About one-third of the arboreal sets were on lianas and branches of <10 cm diameter, whereas the remainder were on substrates with diameters of >10 cm. Terrestrial stations included a variety of microhabitats, such as under boulders, by fallen and rotten logs, in front of openings between exposed roots and cavities at tree bases, and in open understory forest with either a dense growth of Acanthaceae ground cover or thick leaf litter. The nearly even proportion of arboreal versus ground captures contrasts with trapping results in the RS d'Anjanaharibe-Sud, where only one of six *E. tanala* was captured in an arboreal setting (Goodman & Carleton, 1998).

As in the RS d'Anjanaharibe-Sud, the distribution of this species along trap lines appeared to be clumped (Goodman & Carleton, 1998). For example, in the 1500 m zone of the RNI d'Andohahela, five of eight *E. tanala* were captured within a 30 m section of a trap line that was 454 m long.

No differences in level of breeding activity were apparent within and between the various elevational zones during the 2-month period of the survey. Animals trapped at most sites varied in age and condition—from young males with abdominal testes to adult males with large scrotal testes and convoluted epididymides, and from immature females with imperforate vaginas to adults

carrying embryos or bearing placental scars. No female, however, was actively lactating. The ratio of adult to subadult individuals was 4:4 at 810 m, 4:1 at 1200 m, and 6:5 at 1500 m (Table 14-6). Of the females dissected, one had four embryos measuring 19 mm crown-rump length and one had three placental scars. The mammae formula was 1-0-2 ($n = 7$), although one individual deviated from this and had a formula of 1-1-1.

COMMENTS—The examples of *E. tanala* from the RNI d'Andohahela average smaller in most external and cranial dimensions compared to more northern populations, particularly those from the RS d'Analamazaotra (18.5°S) and RS d'Anjanaharibesud (14.7°S). In their uniformly gray venter and general size, the Andohahela specimens more closely resemble those from the RNI d'Andringitra (22.3°S) and the vicinity of Vinanitelo (21.7°S). The latter place is the type locality of the species. Carleton and Goodman (1998) attributed these slight size and pelage differences to geographically clinal variation, from smaller in the south to larger in the north.

SPECIMENS EXAMINED—Parcel 1, 12.5 km NW of Eminiminy, 24°35.6'S, 46°44.3'E, 810 m (FMNH 156514, 156528, 156631–156636, 156641; UA-SMG 7496); parcel 1, 13.5 km NW of Eminiminy, 24°35.0'S, 46°44.1'E, 1200 m (FMNH 156637, 156638; UA-MP 24, 25; UA-SMG 7544, 7549); parcel 1, 15.0 km NW of Eminiminy, 24°34.2'S, 46°43.9'E, 1500 m (FMNH 156515–156521, 156531, 156532, 156639, 156640).

Eliurus webbi Ellerman, 1949

DISTRIBUTION—Although it was discovered relatively late in the taxonomic history of Nesomyinae (Ellerman, 1949), and even then acknowledged only as a subspecies, *E. webbi* is emerging as one of the most common and geographically widespread rodents of the eastern humid forest. As of 1994, the species was reported from the region of Montagne d'Ambre in the north, and south to the area around Vondrozo and Manombo (south of Farafangana) (Carleton, 1994). The species generally occupies lowland rain forest, ranging in elevation from near sea level to about 800 m, but exceptional records include 1000 m on Montagne d'Ambre and 1525 m on the mountains east of Ivohibe (Carleton, 1994; Goodman et al., 1996a).

Within the RNI d'Andohahela, *E. webbi* inhab-

its lowland forest of parcel 1 between 440 and 810 m. At the lower elevation it was the only species of rodent, native or exotic, trapped during the survey. Other recent fieldwork in southeastern Madagascar has demonstrated that this species is ubiquitous in the remaining relatively intact littoral forests (Manafiafy, Itapera, and Mandena); in lowland forests resting on lateritic soils. (Marovony, Analalava, and Nahampoana); and in marginally upland areas of forest also resting on lateritic soils (Manantantely and Marosohy). At the Marosohy locality, near the northeastern boundary of parcel 1 of the RNI d'Andohahela, the QIT-FER team trapped this species between 350 and 900 m.

ECOLOGY AND REPRODUCTION—There was considerable disparity between the 440 and 810 m zones in the proportion of arboreal versus ground captures of *E. webbi*. At 440 m, 12 of 13 traps yielding *E. webbi* were off the ground, whereas at 810 m only three of six were so positioned (Table 14-4). At 720 m in the RNI d'Andringitra, six of 10 captures issued from arboreal sets; at 810 m this proportion was 11 of 13 (Goodman & Carleton, 1996). Individuals of *E. webbi* were not captured in sympatry with *E. tanala* at either the 440 m site in the RNI d'Andohahela or the 720 m site in the RNI d'Andringitra, but at the next higher elevational station, 810 m in both reserves, the two species were encountered in the same trap lines. Whether consistent patterns exist in the prevalence of terrestrial versus arboreal activities by *E. webbi*, corresponding to the presence or absence of *E. tanala*, will require verification through longer term field studies at single sites.

Of the 12 *E. webbi* captured in arboreal sets within the 440 m zone, one-half were on lianas, branches, or trunks of >10 cm diameter, whereas all three taken in the 810-m zone were on substrates of >10 cm diameter (Table 14-4). Individual *E. webbi* entered live traps placed in a variety of terrestrial microhabitats, from sites in and around boulders and rock outcrops, to forest with open understory but thick herbaceous vegetation or dense leaf litter, and near tree roots. In the 810 m zone one subadult was captured in a pitfall trap (see Chapter 13).

At 440 m, seven of nine males captured possessed abdominal testes and three of five females were reproductively inactive. One female with three placental scars had been lactating. In contrast, all three male *E. webbi* captured at 810 m had scrotal testes, and four of five females exhibited signs of recent or active reproduction. A max-

imum of only 16 days separated trapping activities at these two elevational zones, suggesting a difference in the incidence of breeding of *E. webbi* and perhaps a slightly delayed onset at the higher locality. The mammae formula is consistently 1-0-2 ($n = 6$), except for one individual that appears to lack the postaxial pair and to possess an extra abdominal set (0-2-1).

The breeding schedule appears to vary considerably among populations of *E. webbi*, based on this survey and those in the RNI d'Andringitra and RS d'Anjanaharibe-Sud (Goodman & Carleton, 1996, 1998). In the RNI d'Andringitra (22°S) at 720 and 810 m there was little breeding activity in November and December, whereas in the RS d'Anjanaharibe-Sud (14°S) all eight individuals captured in middle to late October showed some signs of ongoing reproduction. The factors that influence this variation are not known.

COMMENTS—*Eliurus webbi* remains have been identified in pellets from *Asio madagascariensis* collected in the Nahampoana Forest north of Tolagnaro (Goodman et al., 1993). The pellets were collected below a roost within lowland humid forest and close to the ecotone along a cleared agricultural zone.

SPECIMENS EXAMINED—Parcel 1, 8 km NW of Eminiminy, 24°37.6'S, 46°45.9'E, 440 m (FMNH 156513, 156522–156527, 156642–156644; UA-SMG 7419, 7427, 7438, 7444); parcel 1, 12.5 km NW of Eminiminy, 24°35.6'S, 46°44.3'E, 810 m (FMNH 156529, 156530, 156659; UA-MP 19; UA-SMG 7474, 7478, 7481).

Gymnuromys roberti Major, 1896b

DISTRIBUTION—Carleton and Schmidt (1990) summarized the distribution of this relatively rare, or at least seldom collected, species based on only five localities in eastern humid forest that span an elevational belt of 500–900 m. Renewed field efforts have obtained *Gymnuromys roberti* from additional sites: RS d'Anjanaharibe-Sud at 1260 m (Goodman & Carleton, 1998), near Anjozorobe at about 1300 m (Goodman et al., 1998), and the RNI d'Andringitra between 720 and 1625 m (Goodman & Carleton, 1996). Intensive small mammal surveys in the humid forests of the PN de la Montagne d'Ambre have yet to uncover the species so far north (Goodman et al., 1996a, 1997a), leading those authors to suspect that the northern distributional limit is the highland complex around Tsaratanana.

In parcel 1 of the RNI d'Andohahela, one individual of *G. roberti* was captured in the 1200 m zone. This record extends the southern range of the species 200 km beyond its previously reported limit, the MZFAA site 20 km west of Vondrozo (Carleton & Schmidt, 1990). Like *Eliurus tanala* and *Nesomys rufus*, *G. roberti* emerges as another widespread component species of mid-elevation eastern humid forest, although it is apparently not nearly as common as those rodents.

ECOLOGY AND REPRODUCTION—The single individual, a female, was trapped on the ground, along a small mammal runway and next to a cluster of boulders. The animal has large mammae (1-0-2) and two placental scars but contains no embryos.

SPECIMENS EXAMINED—Parcel 1, 13.5 km NW of Eminiminy, 24°35.0'S, 46°44.1'E, 1200 m (FMNH 156614).

Monticolomys koopmani Carleton & Goodman, 1996

DISTRIBUTION—The description of this recently named genus and species is based on four specimens. One (the holotype) was collected in May 1929 on the Ankaratra Massif, around 1800 m and above the Manjakatempo Forestry Station, and three individuals were obtained in 1993 at 1625 m in sclerophyllous forest of the RNI d'Andringitra (Carleton & Goodman, 1996). In February 1996 Goodman and colleagues revisited the Ankaratra Massif and found the species to persist in the Nosiarivo Forest at 2000 m (Goodman et al., 1996b). *Monticolomys koopmani* occurs in parcel 1 of the RNI d'Andohahela at the upper limit of sclerophyllous forest at 1875 m, just below Pic Trafonaomby. Its presence in Andohahela extends the known distribution of the species about 260 km south of Andringitra.

ECOLOGY AND REPRODUCTION—All five individuals of *M. koopmani* collected had triggered live traps placed on the ground (Table 14-4)—on slopes with open understory (three captures), in an area of open understory with thick leaf litter, and along a runway under a moss-covered rock outcrop. In the RNI d'Andringitra, two of three specimens were taken on a liana and the third in a pitfall bucket; the individual recently collected from the Ankaratra Massif was trapped on the ground (Goodman et al., 1996b). These results collectively portray the species as predominantly terrestrial but accessing the lower strata of the for-

est. Because traps were seldom placed more than 3 m above the ground (Table 14-1) it cannot be determined whether *Monticolomys* or other small mammals utilize the mid-strata and canopy portions of Malagasy forest.

At the 1875 m site of parcel 1, individuals of *M. koopmani* appear to be clumped or distributed very locally. Four of five specimens were captured within a 24 m section of a trap line that stretched for 255 m. Two females were taken on consecutive days at one trap station, and a male was captured in a trap 9 m away on one of those days. Microhabitat preferences of the species cannot be gleaned from the coarse habitat variables quantified.

Two of the three males captured had scrotal testes that measured 12×8 mm, with convoluted epididymides on one adult. The third male had partially descended testes that measured 5×3 mm, with nonconvoluted epididymides. Both captured females were adults, but neither bore signs of ongoing reproductive activity. Each had six mammae, distributed as postaxial, abdominal, and inguinal pairs.

COMMENTS—*Monticolomys koopmani* is now known from three mountains (Ankaratra, Andringitra, and Andohahela) in middle and southern Madagascar; a distance of 600 km separates its northernmost and southernmost occurrences in the upper reaches (1625–2000 m) of the eastern humid forest biome. The fragmented distribution of the species conforms to the High Mountain Domain, a phytogeographical unit dominated by sclerophyllous plants that occupy isolated peaks from Andohahela in the south to Tsaratanana in the north (Humbert, 1955). Although populations of *Monticolomys* are now patchily distributed, palynological data suggest that upper montane vegetation once stretched between these peaks as recently as the early Holocene (Burney, 1987, 1997). Its presence in parcel 1 of the RNI d'Andohahela likely approximates the southern geographical limit of the species, but its northern extent remains unknown. No examples of *Monticolomys* were recovered during a small mammal survey of sclerophyllous montane forest in the RS d'Anjanaharibe-Sud, northeastern Madagascar. On this massif, another new genus and species of diminutive nesomyine rodent, *Voalavo gymnocaudus* Carleton and Goodman, 1998, was discovered, filling apparently the same upper montane niche as that documented for *Monticolomys*.

Notwithstanding their present-day discontinuity, the few locality samples of *Monticolomys* are

remarkably similar in size, form, and pelage color. The univariate ranges of most variables, especially craniodental, overlap appreciably (Table 14-7; uniformity of protocol for external dimensions between two different collectors is, of course, suspect), and multivariate analysis of craniodental measurements (PCA) divulged no interpretable discrimination according to geographical origin (results not figured). Although the total number of specimens (10) is insufficient to critically assess patterns of differentiation, the evidence at hand portrays only isolated segments of a single, formerly continuous, montane species.

SPECIMENS EXAMINED—Parcel 1, 20.0 km SE of Andranondambo, $24^{\circ}33.7'S$, $46^{\circ}43.3'E$, 1875 m (FMNH 156534, 156660–156663).

Nesomys rufus Peters, 1870

DISTRIBUTION—*Nesomys rufus* has a broad distribution in eastern, northern, and northwestern forests of the island, occurring from 900 to 2300 m (Carleton & Schmidt, 1990). This relatively large, richly colored nesomyine is not recorded from the PN de la Montagne d'Ambre in the extreme north (Goodman et al., 1996a), but it does inhabit the middle and upper montane forest of the RS d'Anjanaharibe-Sud (Goodman & Carleton, 1998). The southernmost locality of the species had previously been documented in the RNI d'Andringitra, where it was recorded within an elevational range from 810 to 1625 m (Goodman & Carleton, 1996).

The several vouchers of *N. rufus* obtained at 810 and 1200 m in parcel 1, RNI d'Andohahela (Table 14-5), amplify the southern range limits of the species. Furthermore, individual *Nesomys*, presumably referable to *N. rufus*, were observed on a few occasions at 1430 and 1500 m (F Hawkins, pers. comm.). This species overlaps with the lower-elevational form, *N. audeberti*, between 900 and 1000 m in the PN de Ranomafana, where the two are probably the most common members of the local rodent community (Ryan et al., 1993). The QIT-FER small mammal surveys in 1989 and 1990 did not encounter *N. rufus* but did trap *N. audeberti* at several sites in the southeastern region (Marovony Forest and Manantantely Forest).

ECOLOGY AND REPRODUCTION—Previous trapping results and mark-and-release ecological studies indicate that *N. rufus* is a strictly terrestrial rat (Ryan et al., 1993; Goodman & Carleton, 1996, 1998). The three individuals collected in live traps

TABLE 14-7. Selected external and craniodental measurements of *Monticolomys koopmani* from the three massifs of its known geographic occurrence.

Variable	Ankaratra		Andringitra (n = 3)‡	Andohahela (n = 5)¶
	Holotype*	156211†		
TOTL	205.0	245.0	236.3 ± 3.2 234.0–240.0	227.4 ± 7.2 217.0–236.0
HBL	89.0	85.0	98.0 ± 3.6 94.0–101.0	86.2 ± 1.9 84.0–89.0
TL	116.0	150.0	138.0 ± 4.6 134.0–143.0	134.4 ± 5.9 127.0–142.0
HFL	24.0	23.5	24.3 ± 0.6 24.0–25.0	23.6 ± 0.5 23.0–24.0
EL	15.0	19.0	18.3 ± 0.6 18.0–19.0	18.8 ± 0.8 18.0–20.0
WT	—	21.0	26.3 ± 1.1 25.0–27.0	23.0 ± 3.8 19.0–28.0
ONL	26.3	27.1	27.8 ± 0.3 27.5–28.1	27.5 ± 0.4 26.9–28.0
ZB	—	13.7	13.6 ± 0.5 13.1–14.1	13.6 ± 0.3 13.3–14.1
BBC	12.5	11.2	12.7 ± 0.5 12.4–13.2	11.2 ± 0.1 11.1–11.3
IOB	3.9	4.0	4.0 ± 0.1 3.9–4.0	4.0 ± 0.1 3.9–4.1
LR	8.5	9.3	9.9 ± 0.3 9.6–10.2	9.5 ± 0.1 9.4–9.6
BR	4.2	4.6	4.7 ± 0.2 4.5–4.9	4.6 ± 0.1 4.4–4.7
PPL	8.7	9.1	9.5 ± 0.2 9.3–9.7	9.4 ± 0.3 9.1–9.7
LBP	3.7	4.2	4.2 ± 0.2 4.0–4.4	3.8 ± 0.3 3.4–4.0
LIF	5.3	4.6	5.2 ± 0.1 5.1–5.3	5.1 ± 0.2 4.9–5.4
BIF	2.0	1.9	2.0 ± 0.1 1.9–2.0	2.0 ± 0.1 1.9–2.1
LD	7.2	7.7	7.9 ± 0.1 7.7–8.0	7.6 ± 0.2 7.3–8.0
BM1s	5.7	5.5	5.9 ± 0.1 5.8–6.0	5.7 ± 0.1 5.6–5.9
DAB	4.4	4.9	4.8 ± 0.1 4.7–4.9	4.7 ± 0.1 4.6–4.9
BZP	2.2	2.2	2.2 ± 0.1 2.1–2.2	2.3 ± 0.2 2.0–2.4
BOC	6.4	6.1	6.6 ± 0.2 6.5–6.8	6.4 ± 0.1 6.3–6.6
LM1-3	3.70	3.35	3.53 ± 0.12 3.42–3.65	3.52 ± 0.06 3.42–3.57
WM1	1.09	1.02	1.09 ± 0.03 1.07–1.12	1.09 ± 0.02 1.07–1.12

* AMNH 100727; Antananarivo Province, Manjakatempo, 1800 m.
† FMNH 156211; Antananarivo Province, Forêt de Nosiarivo, 2000 m.
‡ FMNH 151727, 151899, 151900; Fianarantsoa Province, RNI d'Andringitra, 38 km S of Ambalavao, 1625 m.
¶ FMNH 156534, 156660–156663; Toliara Province, RNI d'Andohahela, 20 km SE of Andranondambo, 1875 m.
Sample parameters are mean ± SD, and range. Refer to Materials and Methods section for abbreviations of variables.

came from sites in open understory with thick herbaceous vegetation or leaf litter, on a slope under a dense growth of ferns, and by a large opening descending into a cavity under the roots of a fallen tree. A fourth individual was obtained in a National live trap set for carnivores.

Population densities of this species, as indexed by trap returns, seem to vary appreciably among

TABLE 14-8. Number of individuals and percent trap success based on all small mammals captured during the first 500 trap-nights within humid forest (parcel 1) and spiny bush (parcel 2) of the RNI d'Andohahela.

Order and species	Humid forest					Total	Spiny bush 120 m
	440 m	810 m	1200 m	1500 m	1875 m		
Lipotyphla							
<i>Microgale cowani</i>					3	3	
<i>Microgale dobsoni</i>			1	1	1	3	
<i>Microgale gymnorhyncha</i>				1		1	
<i>Microgale soricoides</i>			1		3	4	
<i>Microgale thomasi</i>		1				1	
<i>Oryzorictes hova</i>					1	1	
<i>Tenrec ecaudatus</i>		1				1	
Rodentia							
Murinae							
<i>Rattus rattus</i>		4		2	1	7	1
Nesomyinae							
<i>Eliurus majori</i>			2	1		3	
<i>Eliurus minor</i>		1	5	4	1	11	
<i>Eliurus myoxinus</i>							1
<i>Eliurus tanala</i>		8	2	4		14	
<i>Eliurus webbi</i>	10	5				15	
<i>Gymnuromys roberti</i>			1			1	
<i>Monticolomys koopmani</i>					2	2	
<i>Nesomys rufus</i>			1			1	
Carnivora							
<i>Galidictis fasciata</i>			1	2		3	
Total individuals	10	20	14	15	12	71	2
Percent trap success	2.0	4.0	2.8	3.0	2.4	2.8	0.4
Total Rodentia	10	18	11	11	4	54	2
Percent rodent trap success	2.0	3.6	2.2	2.2	0.8	2.2	0.4
Total Nesomyinae	10	14	11	9	3	47	1
Percent nesomyine trap success	2.0	2.8	2.2	1.8	0.6	1.9	0.2

sites in the eastern humid forest. In the RS d'Anjanaharibe-Sud, the greatest trap success was in the 1260 m zone, with eight animals captured in 500 trap-nights (1.6%) (Goodman & Carleton, 1998); in the RNI d'Andringitra the best results were 11 individuals in 625 trap-nights at 1210 m (1.8%) and 14 animals in 650 trap-nights at 1625 m (2.2%) (Goodman & Carleton, 1996). There were only two individuals in 500 trap-nights (0.4%) in the RNI d'Andohahela (Table 14-8). These biological inventories followed the same trapping protocol and were conducted at approximately the same time of the year. Along with additional information from the PN de Ranomafana, the data thus suggest that *Nesomys rufus* is more common in the middle segment of eastern humid forest but is more rare in the southern portion of this biome. Such an inference does not appear to be a spurious reflection of chance variation in trap success. When *Nesomys* are present in any numbers within a forest, their diurnal ac-

tivities, animated scuffling along the forest floor, and relatively large size readily draw an observer's attention. The species was both visibly rare and infrequently trapped in parcel 1 of the RNI d'Andohahela.

Both of the male *N. rufus* that were captured had large scrotal testes, and both females each contained two embryos measuring between 8 and 10 mm in crown-rump length. A similarly common incidence of breeding activity was also documented during the RNI d'Andringitra and RS d'Anjanaharibe-Sud surveys (Goodman & Carleton, 1996, 1998). Thus, depressed reproduction does not solely account for the variation in trap success between these localities and the apparently low population level noted in the RNI d'Andohahela. The two females have a mammae count of 0-1-1.

SPECIMENS EXAMINED—Parcel 1, 12.5 km NW of Eminiminy, 24°35.6'S, 46°44.3'E, 810 m (FMNH 156645, 156646); parcel 1, 13.5 km NW

of Eminiminy, 24°35.0'S, 46°44.1'E, 1200 m (FMNH 156535, 156647).

Discussion

During fieldwork conducted between 20 October and 4 December 1995, small mammals were censused in all three parcels that compose the RNI d'Andohahela. Previous faunal reports for the reserve do not list any species of Nesomyinae (O'Connor et al., 1987; Nicoll & Langrand, 1989). The 92 specimens (captured in small mammal live traps) of the eight nesomyine species reported herein thus represent the first vouchered evidence of native rodents within the boundaries of the reserve (Table 14-5). Unlike recent field studies of the RNI d'Andringitra and RS d'Anjanaharibe-Sud (Carleton & Goodman, 1996, 1998), however, the biological survey of the RNI d'Andohahela did not uncover any mammals new to science. This may be an indication that our understanding of Malagasy rodent diversity is approaching biological reality, at least for those nesomyines that inhabit the eastern humid forest (see Carleton & Goodman, 1998, for elaboration).

The specimens listed above form the empirical basis for the discussions that follow, and those gathered through the earlier field efforts of Webb, Hoogstraal, MZFAA, and QIT-FER are generally referenced where appropriate to clarify and corroborate our summaries. We concentrate on results obtained for parcels 1 and 2, given the longer period and greater number of trap-nights devoted to those surveys.

Trapping Effort and Sampling Confidence

Collecting effort was disproportionate among the reserve's three parcels, totaling 4,935 trap-nights in parcel 1, 750 in parcel 2, and only 150 in parcel 3 (Table 14-1). In parcel 1, eight species of rodents (Table 14-5), all of which are endemic Nesomyinae except *Rattus rattus*, were documented over a 1435 m elevational band that encompassed lowland forest (440 m), a zone transitional between lowland and montane forest (810 and 1200 m), montane forest (1500 m), and sclerophyllous forest (1875 m). In contrast, indigenous rodent diversity is notably lower in the drier plant communities that dominate parcels 2 and 3 of the reserve (Table 14-5). In the spiny bush and

gallery forest (120 m) of parcel 2, only two rodent species were captured: one nesomyine (*Eliurus myoxinus*) and one introduced murine (*Rattus rattus*). The brief visit to transitional forest of parcel 3 (170 m) also yielded just one species of Nesomyinae (*E. myoxinus*), as well as the two *Rattus* commensals (*R. rattus* and *R. norvegicus*). Tenrecid insectivores regularly entered live-trap lines intended for rodents (Table 14-8; and see Chapter 13); carnivores did so occasionally, but no lemur species was captured in such traps.

Trap success of small mammals—native and introduced rodents, insectivores, and carnivores—varied little among the five elevational stations of parcel 1, ranging from 2% (440 m) to 4% (810 m) as calculated for the standardized trapping period (Table 14-8). The rates based on overall trap success, the grand total of 4,395 trap-nights, differ only trivially: 2.1% (18 animals in 845 trap-nights) at 440 m, 3.1% (26 animals in 850 trap-nights) at 810 m, 2.8% (22 animals in 775 trap-nights) at 1200 m, 3.0% (31 animals in 1,050 trap-nights) at 1500 m, and 2.9% (25 animals in 875 trap-nights) at 1875 m. The relative homogeneity of trap returns across elevations in the RNI d'Andohahela contrasts with results recorded in similar montane transects conducted elsewhere in Madagascar. For example, in the RNI d'Andringitra and RS d'Anjanaharibe-Sud, capture rates were distinctly higher over mid-elevations (ca. 1000–1500 m), ranging from 6 to 10% (Goodman & Carleton, 1996, 1998). The trapping results from RNI d'Andohahela conform with those previously reported in one respect: the poorest success was obtained at the lowest elevation surveyed in each transect, sites (440–875 m) situated within lowland rain forest or near its transition to montane forest. Small mammal trap success in parcel 2 was especially meager, 0.4% realized during 750 trap-nights (Table 14-8), but the short duration of trapping and the paucity of comparable field studies in such dry habitats do not permit meaningful generalizations.

The cumulative number of rodent species captured at each elevational zone of parcel 1 became asymptotic well before the termination of a trapping session (Fig. 14-3, top). The expenditure of sampling effort at which these various plateaus were attained varies considerably—250 trap-nights at 440, 1200, and 1500 m; 500 trap-nights at 1875 m; and 625 trap-nights at 810 m. Similarly, there was substantial variability in capture results over the course of trapping at each elevation; there was no suggestion of orderly diminish-

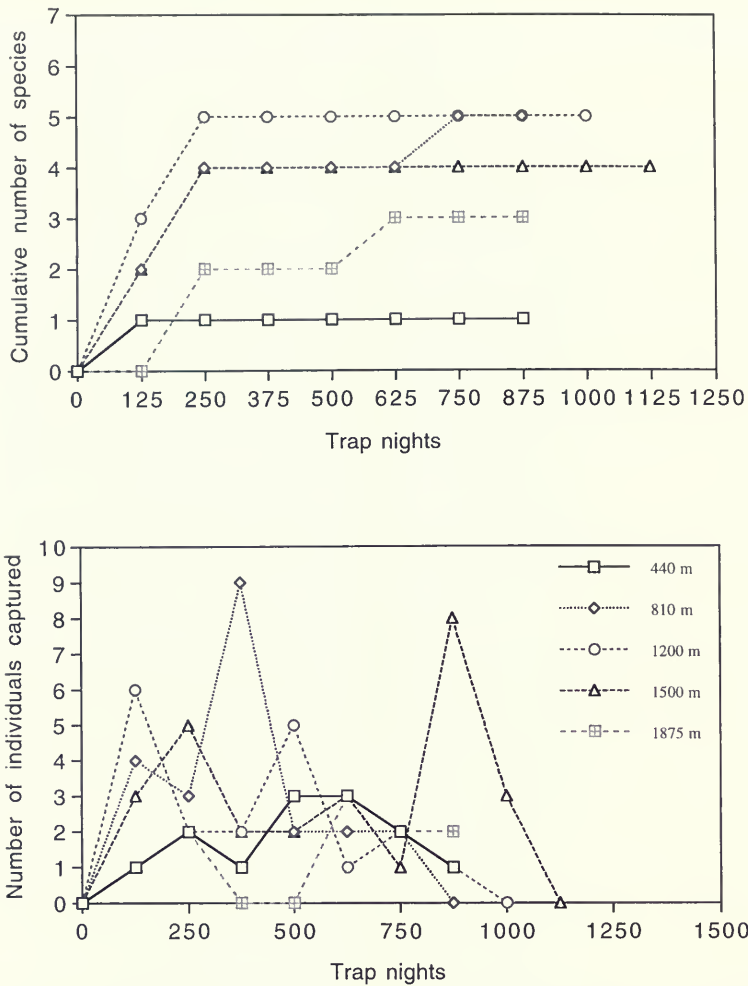


FIG. 14-3. Plots of trap-nights against the cumulative number of rodent species obtained (**top**) and against the number of individuals trapped (**bottom**) for the five elevations surveyed within parcel 1, RNI d'Andohahela (results include all nesomyine species and *Rattus rattus*).

ing rates as the survey progressed, nor was there any correspondence to the asymptotic levels that were eventually reached (Fig. 14-3, bottom). The leveling of these species accumulation curves therefore does not appear to result simply from reduction in trap success.

Although species accumulation curves stabilized over the 7 weeks of fieldwork, the knowledge of nesomyine distributional patterns gained over the past decade predicts that the number of forms resident in the reserve will be increased by at least two, perhaps three. These include one species associated with dry habitats, *Macrotrarsomys bastardi*, and two species found in moist areas, *Brachytarsomys albicauda* and *Nesomys audeberti*.

Macrotrarsomys bastardi is a denizen of dry deciduous forests and arid bush and thicket formations in western and southern Madagascar (Carleton & Schmidt, 1990). Webb had collected the species at 5 mi E Bevilany (his series is in BMNH), and the QIT-FER team discovered it in the Petriky Forest, 5–7 km southeast of Manambaro (series are in UADBA and USNM). Parcels 2 and 3 of the RNI d'Andohahela are close to these localities, particularly the Bevilany site, and they contain habitat suitable for *Macrotrarsomys*. Furthermore, the presence of *Eliurus myoxinus* within parcels 2 and 3 (see species account) underscores our expectation that *M. bastardi* will yet be found, because the two species commonly occur at the same localities elsewhere in Madagascar

(Carleton & Schmidt, 1990). At other dry forest sites, its capture has proved highly variable and may relate to the cyclical availability of foods and corresponding population densities (Randrianjafy Rasoloarisoa, 1993; Ganzhorn et al., 1996; Goodman & Rasoloarison, 1997). Under such circumstances, a species such as *M. bastardi* could have been easily overlooked during the abbreviated fieldwork in parcels 2 and 3.

Brachytarsomys albicauda was not trapped in the RNI d'Andohahela, but there is some evidence that this large, arboreal species is resident there. A villager from Enosiary, at the eastern limit of parcel 1, assisted the 1995 mission. He remembered that several years earlier, while traversing at night the humid forest along the Col de Tanatana between Isaka-Ivondro and Eminiminy, he had encountered a lemur-like animal moving along a system of vines. It was captured approximately 1 m off the ground, killed, roasted, and eaten.¹ His description of the animal aptly fits the salient characters of *B. albicauda*.

The Col de Tanatana is at about 750 m, which is within the known altitudinal range of *Brachytarsomys albicauda* (Carleton & Schmidt, 1990). To date the southern limit of the species has been noted as eastern humid forest in the vicinity of Vinanitelo and Ikongo (Carleton & Schmidt, 1990), approximately 300 km northeast of the Col de Tanatana. Curiously, no specimens of *Brachytarsomys* were recovered in the survey of the RNI d'Andringitra (Goodman & Carleton, 1996), nor did the QIT-FER team collect any in their sampling of several lowland and littoral forests in southern Madagascar. A museum specimen, its identification confirmed by comparison to type material, would do much to resolve the question of the species' existence in the RNI d'Andohahela.

The third species of possible occurrence in the RNI d'Andohahela is *Nesomys audeberti*. Like *N. rufus*, it is a large and conspicuous diurnal rodent. This nesomyine has been previously recorded in southeastern Madagascar, from lowland forest covering lateritic soils. Sites include a ridge west

of Vondrozo at 500 m (MZFAA series in AMNH, BMNH, and MNHN), Manombo near sea level (MZFAA specimen in MNHN), the Bemangidy Forest below 100 m (Hoogstraal specimen in USNM), and the Marovony Forest at 50 m and Manantately Forest at 100–450 m (QIT-FER series in UADBA and USNM; Fig. 14-2). Our failure to catch *N. audeberti* in parcel 1 and the same result for the QIT-FER team in the Marosohy Forest along parcel 1 may indicate that its preferred habitats are not found within this section of the RNI d'Andohahela. Populations of *N. audeberti* may be contained in other sections of parcel 1, such as the magnificent low-lying forest, with its strikingly different plant composition, that covers the headwaters of the Manampanihy Basin.

A fourth nesomyine, a giant species known only from subfossil remains, deserves mention here. *Hypogeomys australis*, a congener of *H. antitena*, from west-central Madagascar, was named based on material excavated from Andrahomana Cave, 40 km west of Tolagnaro (Grandidier, 1903). A bone of *H. australis* from the type locality has yielded a radiocarbon date of 4,440 ± 60 BP (Goodman & Rakotondravony, 1996). If this species had survived into recent times, such a unique and imposing animal would certainly be retained in the rich folklore of the Antanosy and Antandroy tribes, if not mentioned in the earliest historical accounts (Flacourt, 1658).

Along with *Rattus rattus* and *R. norvegicus*, a third commensal murine, *Mus musculus*, is common in lowland villages and agricultural settings, but we lack evidence that it enters natural forest within the reserve. In the Nahampoana Forest, north of Tolagnaro, this rodent was identified in regurgitated pellets from *Asio madagascariensis* collected at the edge of lowland forest not far from agricultural lands (Goodman et al., 1993). This owl is believed to be largely forest-dwelling (Langrand, 1995), in which case the *Mus* could have been killed within the forest or along its edge.

In summary, we are confident that the seven nesomyine species actually trapped in parcel 1, a tract of eastern humid forest, represent nearly all of those plausibly expected to inhabit forest at this latitude. The completeness of documentation for parcels 2 and 3 of the RNI d'Andohahela is justifiably suspect, given the short duration of fieldwork at those sites and our awareness of the probable occurrence of one other species within such dry habitats in southeastern Madagascar.

¹ Normally the consumption of rodent meat is strictly taboo to most Malagasy, but lemur is eaten by certain cultural groups (Ruud, 1970). The Enosiary guide recounted the moment after the animal was killed and the factors that prompted his decision to eat it. He was convinced that it was a lemur by the way it moved and its general behavior, and he was very hungry. He was somewhat perplexed by the animal's rodent-like teeth, particularly the front incisors, but he finally decided that it was lemur-like enough to be properly edible.

Elevation and Rodent Associations

ELEVATIONAL DISTRIBUTION—No rodent species was trapped at all five stations along the elevational transect of parcel 1, RNI d'Andohahela (Table 14-5). *Eliurus minor*, recorded at the four sites between 810 and 1875 m, appears to occupy the broadest band among native species within the reserve, a finding that agrees with its elevational occurrence as noted elsewhere on the island (Carleton & Schmidt, 1990; Goodman & Carleton, 1996). *Eliurus tanala* populates middle elevations (810, 1200, and 1500 m) and is found sympatrically with *E. webbi* at the lower zone and with *E. majori* at the two upslope sites. Other species were obtained in just one or two of the transect sites. Such examples of restricted occurrence may be only an artifact of unsuccessful trapping (*Gymnuromys roberti* and *Nesomys rufus*) or mirror real affinity to a particular vegetation class (*E. webbi* in lowland rain forest, *E. majori* in montane forest, and *Monticolomys koopmani* in sclerophyllous montane forest). Introduced *Rattus rattus* was trapped in essentially pristine forest at all sites except those at 440 and 1200 m; further trapping will likely reveal the species as ubiquitous in primary forest of the reserve.

The elevational juxtaposition of the three large *Eliurus* species in parcel 1 corroborates survey results for other forested mountain slopes in eastern Madagascar. *Eliurus webbi* was not only relatively abundant at 440 m but the only species recorded at that elevation. At 810 m, however, it was outnumbered by individuals of *E. tanala* by a ratio of 8:5. At 1200 m *E. webbi* is not part of the local rodent fauna, but *E. tanala* and *E. majori* do co-occur there and at 1500 m (Table 14-5). The altitudinally contiguous allopatry observed for *E. webbi* (440–810 m) and *E. majori* (1200–1500 m), with populations of *E. tanala* overlapping each of those species, repeats the pattern found in both the RNI d'Andringitra and RS d'Anjanaharibe-Sud (Goodman & Carleton, 1996, 1998). It is interesting that to date the only place where *E. webbi* and *E. majori* have been collected in sympatry is at 1000 m in the PN de la Montagne d'Ambre, an outlier mountain not inhabited by *E. tanala* (Goodman et al., 1996a). Whether these instances of altitudinal replacement among congeneric rodent species represent interference competition or reflect fine-grained microhabitat requirements will require detailed long-term ecological investigation.

As noted above, the elevational fidelities of cer-

tain rodents in parcel 1 naturally correspond to previously recognized, broadly defined forest types. For example, *Eliurus webbi* occurs in lowland rain forest; *E. tanala*, *E. majori*, and *Nesomys rufus* are encountered in the lowland-montane transitional zone through the upper reaches of montane forest (the infrequently trapped *Gymnuromys roberti* may belong here as well); *Monticolomys koopmani* inhabits sclerophyllous montane forest; and *E. minor*, apparently the most eurytopic nesomyine, ranges broadly across all of these elevations and forest associations. Although the montane rodent communities of Madagascar exhibit some altitudinal zonation, they seem to lack the sharply defined stratification documented in other tropical areas (Pearson & Ralph, 1978; Rupp, 1980; Patterson et al., in press). In part, this modest zonal partitioning may simply reflect the absolutely fewer rodent species found on Madagascar as compared to their greater numbers along the eastern flanks of the Andes in South America or on the slopes of the rift mountains in East Africa.

A notable omission, however, among Madagascar's endemic rodents consists of those species that live exclusively in open habitats above the tree line. Such an alpine contingent forms a rich and distinctive subset of rodent communities that occur on high mountains elsewhere in the New and Old World tropics—for instance, the páramo and puna zones of the Andes (Pearson & Ralph, 1978), the alpine heathlands of the Ethiopian highlands (Rupp, 1980), or the meadowed plateaus that crown New Guinea's mountainous backbone (Flannery, 1995).

No evidence presently exists that such an alpine rodent community differentiated on Madagascar. This absence seems to be an accident of Malagasy geology; there are no massive tablelands rising above 3000 m that would suit the formation of high-altitude grasslands and foster the evolution of pastoral rodents, their numbers consequently enhancing the zonation of species along an elevational profile. The alpine region surrounding the island's second highest mountain, Pic Boby (2658 m) in the RNI d'Andringitra, contains only the single indigenous species *Brachyuromys betsileoensis* (Langrand & Goodman, 1997). This vole-like form, with small, rounded pinnae and short tail, occurs throughout heathland areas (>2000 m) of the Andringitra Massif but also penetrates contiguous portions of montane and sclerophyllous forest (1700–1900 m); on the same massif, its congener *B. ramirohitra*, equally vole-

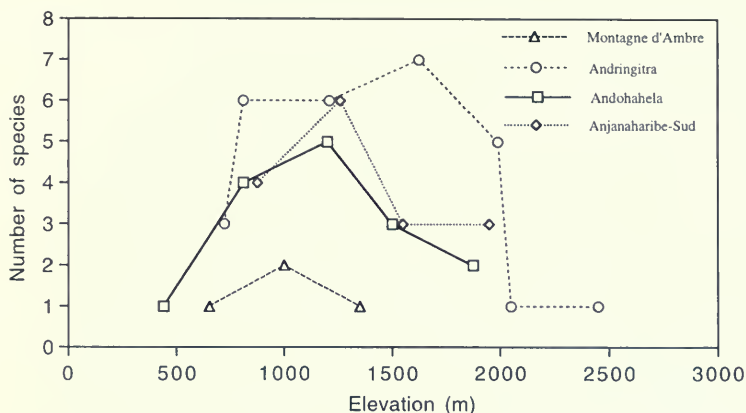


FIG. 14-4. Relationship between number of sympatric native rodents and elevation within four large Malagasy reserves. At each site, the most species occur at elevations within upper montane forest (the mid-elevational “bulge”) and fewer coexist at lower and higher zones.

like in appearance, seems confined to montane forest and the *Aguaria* zone at the upper fringe of sclerophyllous forest (1200–1625 m) (Goodman & Carleton, 1996). Little is known about the small mammal community of the RNI de Tsaratanana (Albignac, 1970), which contains Pic Maromokotro (2876 m), the highest peak on the island. If a guild of uniquely alpine small mammals remains to be discovered on the island, we suspect that it will be found on the slopes just below Pic Maromokotro. This zone, however, has been burned repeatedly since the 1920s (Perrier de la Bâthie, 1927; Humbert, 1928), and the effect of this practice on the small mammal community is uncertain.

SPECIES RICHNESS—In recent years, several hypotheses, not necessarily mutually exclusive, have been advanced to explain the distribution of organisms along latitudinal and altitudinal gradients and the factors that influence them (Rahbek, 1997). One school has stressed the effects of forest productivity in molding these patterns (Ricklefs & Schluter, 1993; Rosenzweig & Abramsky, 1993). A notable example of a species diversity gradient involves the peaking of species numbers at middle elevations on mountains in tropical latitudes, a phenomenon now recorded for a variety of organisms (e.g., Heaney & Rickart, 1990); such hump-shaped species diversity profiles have been related to measures of environmental complexity and ecological productivity (see Rosenzweig, 1992, for review). Numerous variables, taken singly or acting in concert, have been invoked to explain this pattern: rainfall and temperature, solar

radiation, evaporation, water shortage or water logging, and changes in soil nutrients and acidity. Distribution of nesomyine species within parcel 1 of the RNI d’Andohahela conforms to a weakly unimodal, hump-shaped pattern across the five altitudinal zones surveyed (Fig. 14-4; Table 14-5). The greatest nesomyine diversity is five species, recorded at 1200 m within the lower extent of montane forest proper, whereas the fewest species are found at the lowest (one at 440 m in lowland rain forest) and highest (two at 1875 m in sclerophyllous montane forest) sectors trapped; intermediate numbers were documented at the other middle elevational stations—four at 810 m (lowland-montane transition) and three at 1500 m (upper extent of montane forest). Moreover, a mid-elevation bulge in nesomyine species richness is suggested by surveys of several other large mountainous reserves (Fig. 14-4), including the RNI d’Andringitra (Goodman & Carleton, 1996; Langrand & Goodman, 1997; Goodman, unpubl. data), the RS d’Anjanaharibe-Sud (Goodman & Carleton, 1998), and PN de la Montagne d’Ambre (Goodman et al., 1996a). These sites, plus the RNI d’Andohahela, collectively bracket the full latitudinal extent, from 12.5° to 24.5°S, of the eastern humid forest biome in Madagascar (Fig. 14-1), and all were inventoried using the same kinds of traps and sampling protocol. Further, the surveys of Andohahela, Andringitra, and Anjanaharibe-Sud were conducted during the same period of the calendar year (October to early December).

Although a middle elevational bulge in species

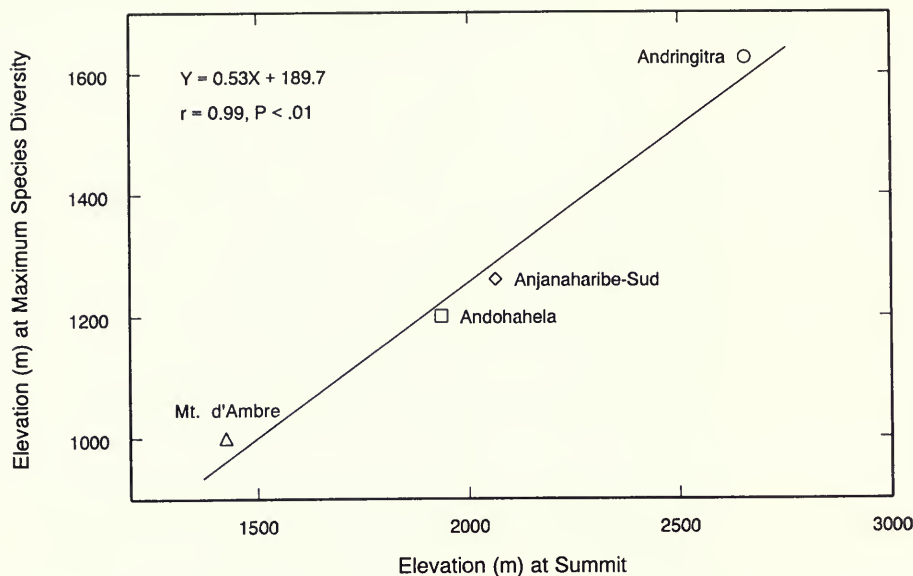


FIG. 14-5. Regression of the elevation with the most native rodent species and height of summit for four reserves within the eastern humid forest biome. The highly significant relationship suggests the interplay of physical relief and orographic factors such as rainfall and cloud cover in explaining the maximal overlap of rodent species along tropical mountain slopes (see text for discussion).

richness recurs among these four mountains, there is no consistent height at which diversity of native rodents peaks (Fig. 14-4). Zones that hold the largest number of species vary from 1000 m on Montagne d'Ambre to 1625 m on the Andringitra Massif. Nor is there an orderly north to south trend, suggestive of slight elevational shifts in vegetational communities along a latitudinal gradient, in the height where maximum species abundance was recorded. The two mountains with species diversity maxima at lower elevations lie at the opposite ends of Madagascar (Montagne d'Ambre, 1000 m, and Andohahela, 1200 m), with higher species counts at higher elevations in between (Anjanaharibe-Sud, 1260 m, and Andringitra, 1625 m).

Instead, there exists a strong, positive correlation ($R^2 = 0.99$, $F = 179.9$, $P < 0.01$) between absolute height at the summit and that elevation on the mountain with the most species (Fig. 14-5). For each of these four Malagasy mountains, the site with the greatest species richness occurs within the belt of wet montane rain forest, a zone below the nearly perennial cloud cap and the sub-alpine (sclerophyllous montane) and alpine habitats it envelopes.

Productivity of rodent populations, as indexed by our measures of abundance and biomass (Table 14-9), inconsistently or obscurely corresponds to

elevation with highest species diversity. The 810 m zone of the RNI d'Andohahela, with three nesomyines in contrast to five at 1200 m, supports the largest standing crop of rodents, with or without the inclusion of data from *Rattus* (Fig. 14-6). This disconnection between elevation of greatest species richness and that of the largest total biomass departs from results obtained in the RNI d'Andringitra and RS d'Anjanaharibe-Sud, where all measures of rodent abundance—species diversity, population density, and biomass—were logically and closely coupled within a single elevation (Goodman & Carleton, 1996, 1998). One factor for the biomass–diversity disagreement within Andohahela may involve the inordinately low population density of *Nesomys rufus*, a large-bodied rodent that was numerically abundant in montane zones of Andringitra and Anjanaharibe-Sud and whose heft (adult weight = 150–200 g) contributed substantially to biomass estimates within those reserves.

Nor do elevational zones with the largest value of rodent biomass clearly relate to summit height for the three Malagasy reserves surveyed during approximately the same yearly interval (data from PN de la Montagne d'Ambre, obtained during a different time period, are excluded). Again, a non-relationship is generally disclosed whether individuals of *Rattus* are included or excluded. Our

TABLE 14-9. Estimated biomass (g) of rodents trapped along an elevational transect in parcel 1 of the RNI d'Andohahela.

Species	Elevation (m)				
	440	810	1200	1500	1875
<i>Rattus rattus</i>		578		289	289
<i>Eliurus majori</i>			199	100	
<i>Eliurus minor</i>		39	193	154	39
<i>Eliurus tanala</i>		754	189	377	
<i>Eliurus webbi</i>	883	442			
<i>Gymnuromys roberti</i>			120		
<i>Monticolomys koopmani</i>					45
<i>Nesomys rufus</i>			182		
Number of species	1	4	5	4	3
Total biomass (g)	883	1,813	883	920	373
Total biomass (g) excluding <i>Rattus</i>	883	1,235	883	631	84

The numerical data represent summations from the average weight of adults captured over the first 500 trap-nights within each zone.

biomass comparisons among elevations and between major reserves hinge critically on line-transect, removal-trapping results, which can be notoriously happenstance and embrace unknown but likely high levels of sampling error. Furthermore, some studies have shown that nesomyine species undergo seasonal reproductive cycles and population fluctuations (Rakotondravony, 1992; Stephenson, 1994; Goodman et al., 1997a), annual phenomena which our short-term calculations of biomass would overlook. Whether rodent population density and biomass on Madagascar's mountains predictably conform to some larger pattern will require specifically designed field investigation, conducted over a longer term and preferably employing a grid-based, mark-and-release scheme.

In summary, the peak of rodent species richness in Madagascar's eastern humid forest consistently occurs within middle to upper montane vegetation, a band which coincides with that portion of a mountain just below the zone of frequent cloud cover. The absolute height of a mountain, and its physical effect upon cloud formation and rainfall pattern, influences the vertical position of the montane zone and accounts for the significant positive correlation between elevation with the most rodent species and height at the summit (Fig. 14-5). In turn, topography and the related orographic variables of rainfall and cloud cover strongly modulate processes such as water transfer, penetrance of solar radiation, nutrient cycling, and richness of the soil macrofauna. Acting in concert, such variables may locally optimize eco-

logical productivity along a mountainside and partly explain the mid-elevational bulge in rodent species richness.

INTRASPECIFIC AND INTERSPECIFIC DIFFERENCES IN REPRODUCTION—Over the past few years new information has become available on the reproductive ecology of nesomyine rodents. Most of this work is associated with differences in the age and reproductive state of rodents along elevational transects (Goodman & Carleton, 1996, 1998). We hasten to add that although there have been some advances, we know virtually nothing about the cues these animals use to commence breeding cycles. Here we summarize information on the reproductive condition of rodents trapped in the RNI d'Andohahela and compare this information to parallel transects on the slopes of the RNI d'Andringitra and the RS d'Anjanaharibe-Sud.

Levels of rodent reproduction were generally high on the slopes of parcel 1 of the RNI d'Andohahela, with signs of active breeding evident in 36% (440 m) to 94% (1220 m) of the animals trapped within an elevational zone (Table 14-6). Moreover, no progressive trend with elevation is suggested for these data. In the RNI d'Andringitra there was a directional pattern of increasing reproductive activity at higher altitudes, ranging from only 25% of the rodents sampled at 720 m to over 80% at 1625 m. This trend is not evident in the data from RS d'Anjanaharibe-Sud.

These three elevational transects were made at slightly different periods: parcel 1 of RNI d'Andohahela from late October through early

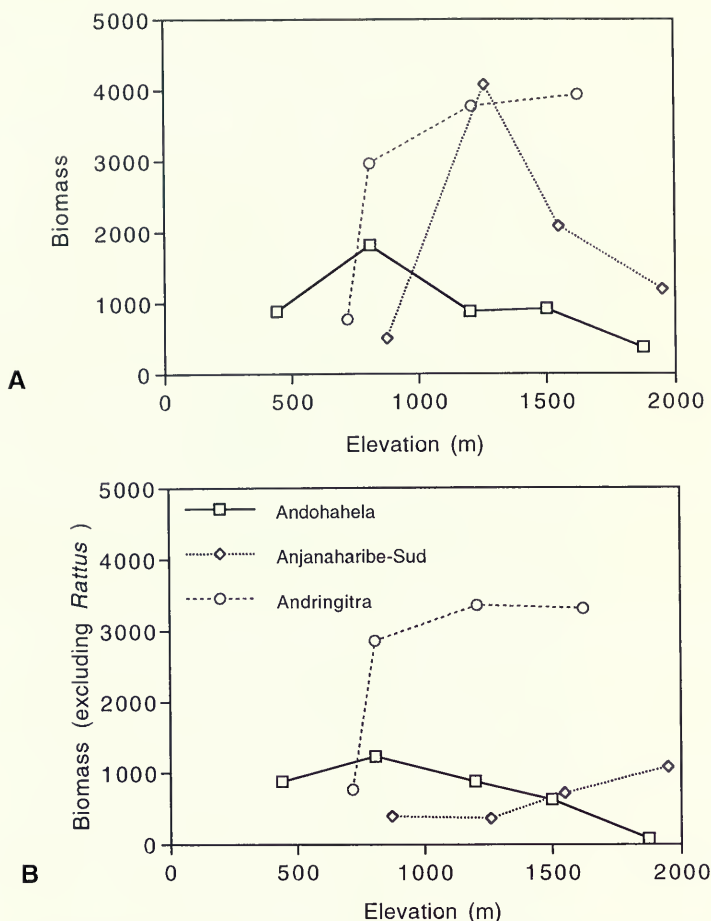


FIG. 14-6. Plots of elevation against rodent biomass for animals captured during the first 500 trap-nights for three mountains in the eastern humid forest: (A) biomass based on all rodents captured; (B) biomass based only on nesomyine rodents.

December, RNI d'Andringitra from middle November through middle December, and RS d'Anjanaharibe from middle October through November. Overall in each of these surveys and across all elevational zones, adults made up 70%, 95%, and 61% (respectively) of the animals captured. These patterns cannot be simply explained by differences along a north-south gradient; Andringitra, which is at middle latitudes relative to the other two sites, had the lowest percentage of subadults. Furthermore, differences between the surveys relative to the calendar year are subtle enough that the observed differences between Andringitra and the other two sites cannot be easily explained. In addition, the Andringitra survey ran the latest into December and would be expected to have a greater percentage of young animals. Simple explanations of latitudinal or seasonal gra-

dients are thus insufficient to explain the differences between these sites. The effects of variation in rainfall and food availability are not necessarily related to photoperiod, and therefore seasonal regulation of reproduction in tropical rodents may not reflect a calendrical cycle (Bronson & Heideman, 1994).

Biogeography

Of Madagascar's major biotic provinces, knowledge of nesomyine species is best documented for the eastern humid forest. The firmer foundation of biodiversity for this zone reflects, in part, the easier accessibility of eastern forest to early naturalists in Madagascar and, more importantly, the resurgence of directed field surveys in the past decade. As a

TABLE 14-10. Documentation of nesomyine and murine rodents within six Malagasy nature reserves (arranged from south to north).

Species	Andohahela*		Andringitra†	Ranomafana‡	Analamazotra¶	Anjanaharibe-Sud	Montagne d'Ambre**
	Parcel 2	Parcel 1					
Murinae							
<i>Mus musculus</i>			+	+			
<i>Rattus rattus</i>	+	+	+	+	+	+	+
Nesomyinae							
<i>Brachytarsomys albicauda</i>				+	+	+	
<i>Brachyuromys betsi-leoensis</i>			+	+	+		
<i>Brachyuromys ramirohitra</i>			+				
<i>Eliurus grandidieri</i>						+	
<i>Eliurus majori</i>		+	+			+	+
<i>Eliurus minor</i>		+	+	+	+	+	+
<i>Eliurus myoxinus</i>	+						
<i>Eliurus petteri</i>					+		
<i>Eliurus tanala</i>		+	+	+	+	+	
<i>Eliurus webbi</i>		+	+	+	+	+	+
<i>Gymnuromys roberti</i>		+	+	+	+	+	
<i>Macrotarsomys bastardi</i>	+						
<i>Monticolomys koopmani</i>		+	+	+			
<i>Nesomys audeberti</i>			+	+	+		
<i>Nesomys rufus</i>		+	+	+	+	+	
<i>Voalavo gymnocaudus</i>						+	
Total rodent species	3	8	12	11	10	10	4
Total nesomyine species	2	7	10	9	9	9	3

* This study; *Macrotarsomys bastardi* is included based on its occurrence at nearby Bevilany (specimens in BMNH).
† Goodman and Carleton (1996); Langrand and Goodman (1997); Goodman (unpubl. data).
‡ Ryan et al. (1993); specimens in UADBA and USNM.
¶ Compiled from Carleton and Schmidt (1990) and Carleton (1994).
|| Goodman and Carleton (1998).
** Raxworthy and Nussbaum (1994); Goodman et al. (1996a, 1997a).

result, solid information regarding numbers of species and their elevational distribution has now been collected for six sites, all within established reserves, that together bracket nearly the complete length of the island and include its principal uplands (Fig. 14-1; Table 14-10).

THE SOUTHEASTERN REGION—Of the six sites, the RNI d'Andohahela, with the immense biotic variety embraced by its three parcels, lies farthest to the south and constitutes an unparalleled natural resource that enhances biological understanding of Madagascar's lesser known southeastern region. The 1995 small-mammal survey of the reserve, for example, produced vouchered records that significantly amplify the southern distributional limits for seven species of Nesomyinae (*Eliurus majori*, *E. minor*, *E. tanala*, *E. webbi*, *Gymnuromys roberti*, *Monticolomys koopmani*, and *Nesomys rufus*—see species accounts above),

all of them near the southern terminus of eastern humid forest. These specimens, together with those collected earlier by Webb, Hoogstraal, and the MZFAA and QIT teams, indicate that the native rodent fauna of southeastern Madagascar can be subdivided into four groups according to their preferred habitat, as follows.

(1) Lowland rain forest and humid littoral forest—*Eliurus webbi* and *Nesomys audeberti*, the latter only on slightly higher grounds composed of lateritic soils

(2) Montane forest and transitional forest on foothills—*Eliurus majori*, *E. minor*, *E. tanala*, *Gymnuromys roberti*, and *Nesomys rufus* (with *E. majori* occurring more commonly within upper montane vegetation and *E. minor* penetrating the next higher altitudinal zone)

(3) Sclerophyllous montane forest—*Monticolomys koopmani*

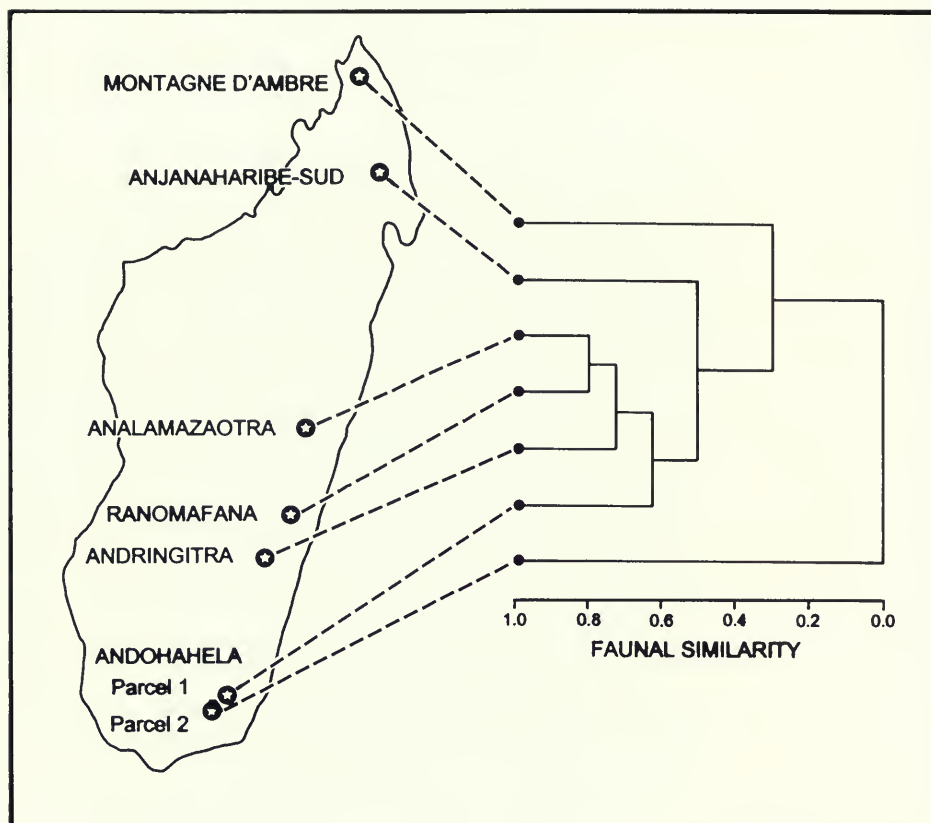


FIG. 14-7. Pattern of faunal similarity (Jaccard Index) based on native rodent species documented at six Malagasy nature reserves and parks. Note the sharp discontinuity between the site in spiny bush forest (parcel 2, RNI d'Andohahela) and the six sites found within moist forest, including parcel 1 of the RNI d'Andohahela (see text for discussion).

(4) Dry deciduous forest and scrub formations—*Eliurus myoxinus* and *Macrotarsomys bastardi*

The dramatic rain shadow and striking floristic transition imposed by the Anosyenne Mountains are emphasized by the complete turnover in species composition of rodents dwelling within or near parcels 1 and 2 of the RNI d'Andohahela (Table 14-10; Fig. 14-7). This abrupt break in nesomyine geographical ranges, across a zone <20 km wide, mirrors the distributional hiatus recorded for so many other organisms found in southeastern Madagascar (see Goodman et al., 1997b, and other chapters in this volume). In effect, the spiny bush of parcel 2—together with other southeastern formations such as the transitional forest of parcel 3, dry littoral forest of Petriky, and spiny bush forest around Bevilany—supports a native rodent community (*Eliurus myoxinus* and *Macro-*

tarsomys bastardi) like that characteristic of western Madagascar.

The nesomyine species of parcel 1 in Andohahela, on the other hand, are typical of those inhabiting humid forest formations throughout eastern Madagascar (Table 14-10; Fig. 14-7). In particular, the association of rodents in parcel 1 most closely resembles (Jaccard Index = 0.70) that documented for the eastern slopes of the RNI d'Andringitra, nearly 300 km to the north. This reserve, situated at the southern end of the Central High Plateau, includes all species known from parcel 1 and a few others (Table 14-10; Goodman & Carleton, 1996). As presently understood, parcel 1 lacks the vole-like species of Andringitra, *Brachyuromys betsileoensis* and *B. ramirohitra*, and the lower elevation *Nesomys*, *N. audeberti*. Future collecting may yet uncover this last species. For example, to the east of the reserve, and

east of the Vohimana Mountains, *Eliurus webbi* and/or *N. audeberti* are known from the moist littoral forests of Bemangidy, Mandena, and Manafiafy. At the southern terminus of these mountains, the Nahampoana and Manantantely forests, resting on lateritic soils close to sea level, also hold the same nesomyine pair. So far only *Eliurus webbi* is known from the 440 m site in parcel 1 of RNI d'Andohahela, which otherwise resembles some of the places listed above in edaphic setting and floristic structure.

THE EASTERN HUMID FOREST BIOME—The assemblage of forest species found in parcel 1 of RNI d'Andohahela constitutes the southern extension of a relatively homogeneous rodent fauna common to the eastern humid forest biome, an elongate formation that parallels Madagascar's eastern coast. Within this biome there is, for instance, greater faunal similarity between the northernmost (Montagne d'Ambre) and southernmost (parcel 1, RNI d'Andohahela) sites, nearly 1400 km apart, than there is between parcels 1 and 2 of RNI d'Andohahela, separated by only 20 km (Fig. 14-7). The strong faunal affinity among these widely separated eastern forest reserves is influenced by the presence of several nesomyine species (namely, *Eliurus majori*, *E. minor*, *E. tanala*, *E. webbi*, *Gymnuromys roberti*, and *Nesomys rufus*) that are broadly distributed across much of this region. Thus, internodal distances between clusters of eastern forest sites are generally short, although the reserves do group sensibly according to geographical proximity.

Range disjunctions within this ecogeographical province occur principally between the various highland regions and account for the orderly latitudinal aggregations from south to north (Fig. 14-7). For example, *Voalavo gymnocaudus* appears to be restricted to northern mountains (Anjanaharibe-Sud and Marojejy), and *Monticolomys koopmani* occurs as fragmented populations in and along the southern Central High Plateau (Ankaratra, Andringitra, and Ranomafana—see below) and in the southern highlands (Andohahela). The recently described *Eliurus grandidieri* is known to date only from Anjanaharibe-Sud and Marojejy in the northern highlands and at one site on the Central High Plateau (Anjozorobe); its hypothesized sister species, *E. petteri*, is reported for three nearby localities in the northeastern Central High Plateau (Carleton, 1994; Carleton & Goodman, 1998). The presence of one or both forms of *Brachyuromys* adds faunal cohesion to the three reserves situated on the Central High Pla-

teau and its eastern fringes (Andringitra, Ranomafana, and Anamalazaotra); neither species is yet documented from far northern or southern highlands (Goodman et al., 1996a; Goodman & Carleton, 1998; this study). Finally, the PN de la Montagne d'Ambre is notable for its biogeographical distinctiveness among the eastern humid forest reserves situated in high mountains, perhaps due to its physical remoteness and recent volcanism (Battistini, 1965; Rossi, 1974). Only three species of *Eliurus* (*E. majori*, *E. minor*, and *E. webbi*) have been recorded on this isolated cone (Goodman et al., 1996a), and several other broadly ranging nesomyines are noteworthy for their absence there (*E. tanala*, *Gymnuromys roberti*, and species of *Nesomys*).

With the much improved documentation of nesomyine geographical and elevational occurrences, a fresh view of their distributional patterns is emerging. Species whose elevational range includes lower montane forest and the contiguous portion of lowland rain forest (transitional formations around 900–1000 m) occupy a broad north-south swath across all or most of the eastern humid forest. Examples include several *Eliurus*, *Gymnuromys*, and species of *Nesomys* (Table 14-10).

The pivotal significance of an altitudinal threshold around 900–1000 m is supported by information from Late Pleistocene and Holocene pollen cores. Such palynological samples, gathered from the Central High Plateau and elsewhere in eastern humid forest, indicate that today's high mountain vegetational communities, dominated by distinctive ericoid sclerophyllous plants, descended to lower elevations during cooler, drier periods of the Quaternary (Burney, 1987; Straka, 1996; Burney, 1997), perhaps as low as 1000 m (Burney, 1997, p. 84). Corresponding depression of montane and montane-lowland transitional communities to lower elevations would have created vast expanses of continuous forest and promoted faunal interchange.

In contrast, nesomyine rodents that typically occur above 1000 m appear to have more limited geographical ranges, at least as currently known (Table 14-11). Three of these species (*Eliurus grandidieri*, *Monticolomys koopmani*, and *Voalavo gymnocaudus*) have been described in just the past few years, underscoring the generally poor biological understanding of Madagascar's uplands (Carleton & Goodman, 1996, 1998). Pleistocene shifts of highland vegetational communities to as low as 1000 m would still have provided dispersal corridors between mountain peaks within major upland blocks for species occurring in such hab-

TABLE 14.11. Occurrence and altitudinal range of rodents documented for five reserves (arranged from south to north) in Madagascar's eastern humid forest.

	Andoha- hela*	Andrin- gitra†	Anjana- haribe-Sud‡	Montagne d'Ambre¶	
Latitude:	24.5°S	22°S	14°S	12.5°S	
Summit:	1935 m	2658 m	2064 m	1475 m	
Elevational range surveyed:	440–1875 m	720–2450 m	875–1950 m	340–1350 m	All sites
Murinae					
<i>Mus musculus</i>		2050			0–2050
<i>Rattus rattus</i>	810–1875	810–2450	875–1950	340–1350	0–2450
Nesomyinae					
<i>Brachytarsomys albicauda</i>			875		450–1300
<i>Brachyuromys betsileoensis</i>		1990–2450			900–2450
<i>Brachyuromys ramirohitra</i>		1210–1990			900–1990
<i>Eliurus grandidieri</i>			1260–1550		1260–1550
<i>Eliurus majori</i>	1200–1500	1210–1990	1260–1950	1000–1350	1000–1990
<i>Eliurus minor</i>	810–1875	720–1625	875–1260	1000	0–1875
<i>Eliurus tanala</i>	810–1500	810–1625	875–1260		455–1625
<i>Eliurus webbi</i>	440–810	720–810	875	650–1000	0–1000
<i>Gymnuromys roberti</i>	1200	720–1625	1260		500–1625
<i>Monticolomys koopmani</i>	1875	1625–1990			1625–2000**
<i>Nesomys audeberti</i>		810			0–1000
<i>Nesomys rufus</i>	810–1200	810–1990	1260–1950		810–2300
<i>Voalavo gymnocaudus</i>			[1200–1600]–1950		[1200–1600]–1950
Number of species of Nesomyinae	7	10	9	3	

* This study.
† Goodman and Carleton (1996); Langrand and Goodman (1997); Goodman (unpubl. data).
‡ Goodman and Carleton (1998).
¶ Raxworthy and Nussbaum (1994); Goodman et al. (1996a, 1997a).
|| Data were derived from a variety of sources, including the references cited above, Carleton and Schmidt (1990) and Goodman et al. (1996b).
** This does not include the record from the PN de Ranomafana at 900 m.

itats. Such a scenario offers a working hypothesis for explaining the occurrence of rodent species in Madagascar's principal mountain ranges, for example, as argued for the highland rodent genera *Monticolomys* and *Voalavo* (Carleton & Goodman, 1996, 1998) and for the high mountain herpetological communities (Raxworthy & Nussbaum, 1996). But there are still exceptions to our generalizations above.

Two anomalies stand out immediately. For one, *Eliurus majori* is an exceptionally widespread denizen of middle to upper montane forest, from Montagne d'Ambre to Andohahela, but it is not yet known below 1000 m. In particular, its presence on Montagne d'Ambre, isolated from other forests by elevations of <500 m, is puzzling and raises questions about the morphological divergence and status of the Montagne d'Ambre population. The other anomalous situation involves the populations of *Monticolomys koopmani* that occur in the RNI d'Andohahela and in areas far-

ther north (RNI d'Andringitra and the Ankaratra Massif) and are separated by a broad area of low mountains and plateaus of <1000 m (Fig. 14-1). Either the lower limit of the sclerophyllous montane zone was appreciably less than 1000 m in the late Quaternary, or the ecological tolerance of the species is broader (or possibly both). The recent capture of a single *Monticolomys* in the transitional zone between lowland and montane vegetation of the PN de Ranomafana, at about 900 m elevation (specimen in UADBA), lends credence to the former interpretation and helps to explain the presence of the species in the RNI d'Andohahela. Phylogeographical analyses drawing on genetic distances between disjunct populations of *Monticolomys* may fruitfully disclose former connections of Quaternary bridges of high montane forest. Such investigations, coupled with study of fossil pollens in Madagascar's southern highlands, including the RNI d'Andohahela, should reveal whether upper montane forest in

this region generally descended to lower elevations than those farther north.

The generality of these biogeographical interpretations for other nesomyine species will still profit from the basic field survey of unknown geographical regions and taxonomic study of poorly known forms. Several species, such as *Brachytarsomys albicauda* in mid-elevation humid forest and *Nesomys audeberti* in lowland rain forest, probably have broader geographical ranges than currently recognized. In like manner, *Brachyuromys betsileoensis* and *B. ramirohitra*, currently known from eastern humid forest along the Central High Plateau, may occur across a broader range under the right ecological conditions. For other species, refined knowledge of distributional patterns will likely unfold with taxonomic revision and improved definition of their morphological limits (e.g., *Eliurus ellermani*, *E. majori*, *E. minor*, and taxa of *Nesomys*). Many of these distributional and taxonomic uncertainties can be illuminated through survey of the low-lying area, much of it below 1000 m, that extends between the Northern Highlands and the Central High Plateau. Although such a research prospectus for nesomyines inhabiting the eastern humid forest biome is daunting, it is not so challenging as that required for rodents occurring in dry, deciduous habitats of western Madagascar. There the knowledge of specific and distributional limits is still too poor to allow researchers to pose meaningful biogeographical questions.

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Chapter 15

Notes on the Bats of the Réserve Naturelle Intégrale d'Andohahela and Surrounding Areas of Southeastern Madagascar

Steven M. Goodman¹

Abstract

Four bat species were collected in the Réserve Naturelle Intégrale d'Andohahela: *Rousettus madagascariensis*, *Miniopterus manavi*, *Mormopterus jugularis*, and *Myotis goudoti*. With the exception of *Mormopterus*, all were obtained in the humid forest portions of the reserve (parcel 1); *Mormopterus* was netted in an area of spiny bush vegetation (parcel 2). The humid forest species are broadly distributed across the island and occur in both forested and disturbed areas. An analysis of the forest-dwelling bat faunas known from several eastern humid forest sites indicates that species richness is low and that there is little change in the community across this region, which covers about 12° of latitude.

Résumé

Quatre espèces de chauves-souris ont été collectées dans la Réserve Naturelle Intégrale d'Andohahela: *Rousettus madagascariensis*, *Miniopterus manavi*, *Mormopterus jugularis*, et *Myotis goudoti*. A l'exception du *Mormopterus*, on les a toutes prises dans les zones de forêts humides de la réserve (Parcelle 1), et le *Mormopterus* a été attrapé par filet dans une zone de végétation broussailleuse et épineuse (Parcelle 2). Les espèces de forêt humide sont largement éparpillées à travers l'île aussi bien dans la région boisée et dans la région perturbée. Une analyse effectuée sur les chauves-souris demeurant dans la forêt, connue dans plusieurs sites de forêt humide à l'Est a indiqué que la richesse des espèces sont faible et qu'il y a presque aucun changement au niveau de cette communauté à travers la région qui couvre presque 12° de latitude.

Introduction

Peterson et al. (1995) recently published a monograph on the Chiroptera of Madagascar that provides one of the most important summaries of the island's bat fauna since it was treated by Dorst (1947a,b, 1948). Although the monograph is based on original fieldwork and a review of previous collections in museums, remarkably few ar-

eas of the island have been worked for bats, and data on the natural history and distribution of most species remain rudimentary. Furthermore, a considerable amount of new information has been collected since the monograph was completed.

Species lists on the bat faunas that occur in the majority of Madagascar's reserves are not available (Nicoll & Langrand, 1989); such basic information on local species is important for management purposes. Recent bat surveys conducted within protected areas such as the Réserve Naturelle Intégrale (RNI) d'Andringitra, RNI de Ma-

¹ Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, IL 60605-2496, U.S.A.

rojeje, Réserve Spéciale (RS) d'Anjanaharibe-Sud, and the Parc National (PN) de Zombitse et Vohibasia are starting to fill this void (Pont & Armstrong, 1990; Rasolozaka, 1994; Goodman, 1996, 1998). Although bat netting was not a major activity during our inventory of the RNI d'Andohahela, data on the few bats that were captured are presented here. Information is also presented on the regional bat fauna, and distributional patterns of forest-dwelling species across the eastern humid forest are briefly summarized.

Materials and Methods

At each of the inventory sites along the elevation transect in the humid forest of parcel 1 and the single site in the spiny bush of parcel 2 (see Chapter 1), 10 mist-nets (12 m long \times 2.6 m high) were erected for 5-day periods as a standardized means of capturing birds (see Chapter 12; Goodman et al., 1997). In all cases nets were placed in the forest understory, with the lowest rung close to or touching the ground. A few bats were collected in the bird nets. Nets were also set up at several sites with the specific intent of capturing bats; these were generally placed across streams or small rivers. Bat nets were attended from dusk to 2000 hr and checked several times during the night.

Netted bats were prepared as specimens that are deposited in the Field Museum of Natural History (FMNH), Chicago, and the Département de Biologie Animale (UADBA), Université d'Antananarivo, Antananarivo. Specimens deposited immediately after the survey in the latter institution have not yet been catalogued and are individually referenced by the collector's field numbers (UADBA-SMG). Most of the bats were prepared as fluid-preserved specimens, and information is not available on internal reproductive organs or skull measurements. Information is also presented on a small collection of bats made in the Tolagnaro area, including in and around the RNI d'Andohahela, by G. Ken Creighton in 1989 and 1990. This collection is housed in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C. The systematic arrangement used by Peterson et al. (1995) is followed here.

Measurements

Measurements were made from animals in the flesh and from prepared crania. The abbreviations and definitions for measurements (all in mm, with the exception of WT) follow.

BBC	breadth of braincase: distance measured across the hamular processes of the squamosal at the point where they border the mastoid bullae
CM	canine-molar length: measured from anterior alveolar border of canine to posterior alveolar border of last molar
EL	ear length: measured from base of the ear (notch) to the distalmost edge of the pinna
FA	forearm length: measured from outside edge of the wrist to outside edge of the elbow (with wing folded)
HF	hind foot length: measured from the back edge of the heel to the end of the longest toe (not including claw)
IOB	interorbital breadth: the minimum distance across the frontal bones between the orbits. In Megachiroptera this was taken in front of the postorbital processes; in Microchiroptera it was taken behind them
ML	mandible length: measured from midpoint of mandibular condyle to anteriormost point of dentary
ONL	occipitonasal length: distance between tip of the nasals and posteriormost edge of the occiput, just above the foramen magnum
TL	tail length: measured from base of tail (at right angles to the body) to end of the distalmost vertebra
TOTL	total length of body and tail: measured from nose tip to end of the distalmost tail vertebra
TR	tragus length: measured from base of tragus to the distalmost tip
WC	width across canines: measured across the exteriormost alveolar base of the upper canines
WT	weight: measured in grams (g) with Pesola spring scales. Animals ≤ 10 g were weighed to the nearest 0.1 g; those between 11 and 100 g were weighed to within 0.5 g

ZB zygomatic breadth: greatest distance between the lateral surfaces of the zygomatic arches.

Species Accounts

Family Pteropodidae

Rousettus madagascariensis Grandidier, 1929

Fifteen individual *Rousettus madagascariensis* were captured at 400 m in a net spanning the Andranohahela River. Most of these individuals were taken early one morning before dawn as they were flying up the river valley. The site was surrounded by intact lowland humid forest and located in a valley below the high peaks of the Anosyenne mountain chain. Upland areas of this region contain numerous rocky outcrops with a variety of nooks and crannies that would provide ideal roosting places for this bat. Lowland areas outside the reserve are largely made up of open agricultural lands. This bat feeds extensively on the fruits of banana (*Musa*, family Musaceae) and litchi (*Litchi chinensis*, family Sapindaceae).

In mid-November 1989 at a site 2 km WNW of Tolagnaro, near the base of Pic St. Louis and in a grove of litchi trees with ripening fruit, Ken Creighton and S.M.G. netted well over 30 *Rousettus madagascariensis* during one night with two standard 12 m mist-nets. The specimens are housed in the USNM. These fruit bats would grasp a ripe fruit in their mouths and fly off to consume it. *Rousettus madagascariensis* has also been netted in parcel 3 of the RNI d'Andohahela (M. Pidgeon, pers. comm.), in the Nahampoana Forest (USNM 577059–577061, 577250–577255), and in the dry littoral forest near Petriky (USNM 578724). It has also been reported from a site 30 km NE of Tolagnaro (Peterson et al., 1995). Measurements of *R. madagascariensis* from the RNI d'Andohahela (Table 15-1) fall within the ranges given by Bergmans (1994) and Peterson et al. (1995) for this species.

REPRODUCTION—The individuals netted in the RNI d'Andohahela represented a variety of age classes, from young individuals with partially unfused finger joints, to adult males and females that were not in reproductive condition, to males with large scrotal testes and pregnant females. Three females were pregnant with young; two of these individuals were adults, with embryos measuring

30 mm crown-rump length, and the third was a subadult (based on skull ossification), with a single embryo measuring 17 mm crown-rump length.

SPECIMENS EXAMINED FROM THE RESERVE—Parcel 1, 8 km NW of Eminiminy, 440 m (FMNH 156495–156498, 156606–156611, UADBA-SMG 7405, 7407, 7410, 7415, 7416).

Family Hipposideridae

Hipposideros commersoni commersoni (E. Geoffroy, 1813)

This species was observed on two occasions in the humid forest portion of the reserve—in the 400 m and 810 m transect zones during night walks in the forest. No individual was captured in the mist-nets. It has been collected in the littoral forest of Manafiafy, north of Tolagnaro (USNM 578738, 578855).

Family Vespertilionidae

Myotis goudoti goudoti (A. Smith, 1834)

Two *Myotis goudoti* were netted in the humid forest of parcel 1. One was captured at dusk in a mist-net placed over a small tributary of the Andranohahela River at 810 m in an area surrounded by transitional lowland/montane forest. The second individual was netted at dusk in a net placed on a ridge crest in primary montane forest at 1200 m. The latter record is apparently rather high for this species, which has generally been collected in lowland areas up to about 800 m (Goodman, 1996). Measurements of these two specimens are presented in Table 15-1.

Several other records of *Myotis goudoti* from the region include the littoral forests of Manafiafy (USNM 578740, 578741) and Mandena (USNM 578739, 578854) and sites on lateritic soils such as the Marovony Forest at 30 m (USNM 577069), Manantantely Forest at 60 m (USNM 577066), and the Nahampoana Forest between 100 and 450 m (USNM 577067, 577068, 577259, 577260, 577262–577264). It has also been collected in transitional and dry forests associated with riverine habitat near the Itaranta River (USNM 577070, 577071) and along the Anosy River near Bevilany (USNM 577261).

REPRODUCTION—One specimen was a male with

TABLE 15-1. Selected measurements of bats collected during the survey.

Species	Age	TOTL	TL	HF	EL	TR	FA	WT
<i>Rousettus madagascariensis</i>	adult (n = 12)	124.0 ± 4.2 117-131	12.5 ± 2.2 9-15	15.3 ± 0.2 14-16	18.6 ± 1.0 17-20	—	69.7 ± 3.2 62-74	53.1 ± 17.4 41.5-71.5
	subadult (n = 3)	118.3 ± 2.3 117-121	12.3 ± 0.6 12-13	14.7 ± 0.6 14-15	18.7 ± 0.6 18-19	—	69.3 ± 1.5 68-71	49.3 ± 1.5 48.5-51.5
	adults (♂, ♂)	100, 89	49, 39	8, 7	15, 16	6.5, —	40, 37	8.2, 5.2
<i>Miniopterus manavi</i>	adults (♂, ♀)	97, 92	42, 46	7, 7	10, 10	6, 6	37, 38	5.3, 8.0
<i>Mormopterus jugularis</i>	adults (♂ ♀)	115, 103	26, 31	7, 7	21, 18	—	37, 37	12.5, 11.0

TABLE 15-1. Continued.

Species	Age	ONL	ZB	IOB	BBC	WC	CM	ML
<i>Rousettus madagascariensis</i>	adult (n = 5)	34.3 ± 1.9 31.0-35.9	21.0 ± 1.7 18.1-22.6	6.8 ± 0.6 6.0-7.4	14.4 ± 0.7 13.5-15.1	7.1 ± 0.5 6.3-7.6	13.4 ± 0.9 12.3-14.3	27.8 ± 1.7 25.1-29.2
	subadult adult (♀)	33.7 14.2	19.2 9.4	6.5 3.1	14.3 7.0	7.0 4.0	13.0 5.8	27.9 11.0
<i>Myotis goudoti</i>	adults (♂, ♀)	13.1, 13.4	7.0, 7.2	3.2, 3.1	6.8, 7.0	3.8, 3.9	5.2, 5.2	10.1, 10.1
<i>Miniopterus manavi</i>	adults (♀ ♀)	15.4, 15.5	10.0, 10.1	3.8, 3.6	8.3, 8.1	4.4, 4.4	5.8, 5.8	11.4, 11.6

Descriptive statistics are as presented mean ± standard deviation and range, and the number of specimens. With the exception of wt (weight, in g), measurements are in millimeters. See text (p. 252) for explanation of abbreviations.

abdominal testes; the other was a female with an open pubic symphysis and large mammae.

SPECIMENS EXAMINED FROM THE RESERVE—Parcel 1, 12.5 km NW of Eminiminy, 810 m (FMNH 156499); parcel 1, 13.5 km NW of Eminiminy, 1200 m (FMNH 156500).

Miniopterus manavi Thomas, 1906

Two individuals of this species were obtained in parcel 1 of the RNI d'Andohahela. One was netted at 810 m within 10 min after dusk over a small tributary of the Andranohahela River. The bare skin around the eye was dull yellow. The second individual was found by A. Raselimanana at 1500 m in a night roost under a small rock overhang. These specimens are assigned to *Miniopterus manavi* on the basis of differences in measurements of Malagasy *Miniopterus* spp. outlined by Peterson et al. (1995) and Hill (1993). *Miniopterus manavi* has also been collected in the Marosohy Forest near the northern limit of the reserve (parcel 1) at about 350 m (USNM 578744, 578745). It has also been reported along the Mandromodromotra River, 16 km NE of Tolagnaro (Peterson et al., 1995) and near Tolagnaro (Hill, 1993). In the USNM there are series of this species taken at other sites in southeastern Madagascar that include the Nahampoana Forest, 7 km NNW of Tolagnaro, between 100 and 450 m (USNM 577102–577119, 577129–577131, 577297–577299, 577302–577307); the Manantanely Forest, 8–12 km WNW of Tolagnaro, between 100 and 450 m (USNM 577096–577101, 577296); the Itapera Forest, approximately 21 km NW of Tolagnaro, and near sea level (USNM 577128); and along the Itaranta River, 20 km WNW of Ranopiso, at 20 m (USNM 577120–577122, 577124, 577125).

REPRODUCTION—The male had slightly descended scrotal testes, and the female had large mammae.

SPECIMENS EXAMINED FROM THE RESERVE—Parcel 1, 12.5 km NW of Eminiminy, 810 m (FMNH 156501); parcel 1, 15.0 km NW of Eminiminy, 1500 m (FMNH 156502).

Family Molossidae

Mormopterus jugularis (Peters, 1865)

Two individuals of *Mormopterus jugularis* were netted over a small river at the edge of par-

cel 2 of the RNI d'Andohahela. On one side of the river was heavily degraded gallery forest and on the other bank slightly degraded spiny bush. *Mormopterus jugularis* has also been collected in the humid portion of southeastern Madagascar north of Manantenina (USNM 577161–577172, 577178–577188) and in drier areas near the Itaranta Forest (USNM 577132–577134), near Beraketa (USNM 577361), and in the Ankapoky Forest (USNM 577313, 577314, 577321, 577322, 577336). This species has a broad distribution across the island and generally roosts in buildings (Peterson et al., 1995).

REPRODUCTION—The two individuals captured were females, one with large mammae and the other with slightly enlarged mammae.

SPECIMENS EXAMINED FROM THE RESERVE—Parcel 2, 7.5 km ENE of Hazofotsy, 120 m (FMNH 156612, 156613).

Other Regional Records

Several other species of Megachiroptera and Microchiroptera bats have been reported or collected in the Tolagnaro area and around the various parcels of the RNI d'Andohahela. The holotype of *Pteropus rufus princeps*, a subspecies not currently recognized, was collected in the Tolagnaro region (Andersen, 1908). This species has been found near Tolagnaro (Peterson et al., 1995), Bemangidy (USNM 317901, 317902), and Manantenina (USNM 578832, 578833). Colonies are also known from Berenty along the Mandrare River (Nicoll & Langrand, 1989) and in the Manafiafy (St. Luce) forest (Goodman, pers. obs.). *Eidolon dupreanum* has been reported from the Tolagnaro region and the Grotte d'Andrahomana, along the coast south of Ranopiso (Peterson et al., 1995).

Among the Microchiroptera several other species have been reported from the region. *Myzopoda aurita*, a member of the endemic family Myzopodidae, was obtained at Antanifotsy, 8 km N of Tolagnaro (Göpfert & Wasserthal, 1995); 4 km SSE and 2–3 km NW of Manafiafy (USNM 578742, 578743, 578856–578858); along the Mandromodromotra River, 15 km NE of Tolagnaro (Peterson et al., 1995); near Bemangidy (FMNH 85237, 92832, 92833); and in the Analava Forest (USNM 577065). The Bemangidy specimens were found “in curled-up central leaf of very large traveller’s palm [*Ravenala mada-*

TABLE 15-2. A comparison of the forest-dwelling bat faunas of several sites in the eastern humid forests of Madagascar.

Species	Site, latitude, and elevational range sampled			
	Andohahela* 24°36'S 400–1875 m	Andringitra† 22°13'S 720–1625 m	Anjanaharibe-Sud‡ 14°45'S 875–1950 m	Marojejy¶ 14°26'S ~500–700 m
<i>Rousettus madagascariensis</i>	+	+	+	+
<i>Emballonura atrata</i>				+
<i>Hipposideros commersoni</i>	+	+		
<i>Triaenops rufus</i>				+
<i>Myotis goudoti</i>	+	+	+	+
<i>Scotophilus robustus</i>				+
<i>Miniopterus fraterculus</i>			+	
<i>Miniopterus manavi</i>	+			
<i>Miniopterus minor</i>		+		
<i>Miniopterus</i> spp.				+
<i>Myzopoda aurita</i>				+
<i>Tadarida pumila</i>				+
Total number of species	4	4	3	8

* Restricted to the humid forest portions of the reserve and based on information presented in this chapter.

† Goodman (1996).

‡ Goodman (1998).

¶ Pont and Armstrong (1990).

|| Apparently several different species were netted and no voucher specimens were collected. Field determinations for this genus are unreliable.

gascariensis, family Strelitziaceae] near river” (H. Hoogstraal, field notes, FMNH). The horse-shoe-shaped pads on the sole and thumb apparently aid this species in moving along and clinging to the leaves. At numerous other sites on the island *Myzopoda* has been captured in heavily degraded areas and at the edge of marshes where *Ravenala* is a dominant species (Schliemann & Maas, 1978; Göpfert & Wasserthal, 1995). There is some evidence, however, that *Ravenala* is not the only plant used for roost sites. I captured two of the USNM specimens from Manafiafy mentioned above at dusk in mist-nets placed at understory level and within relatively intact littoral forest. These nets were at least 500 m from any *Ravenala*, and it was my impression that the individuals were leaving a nearby roosting site and flying in the direction of the open marshland.

Other species of Microchiroptera known from the area include *Emballonura atrata* (Emballonuridae), collected near the Marovony Forest (USNM 577062, 577063, 577257, 577258), north of Manantenina, and near Fanjahira, on the western side of the Vohimena Mountains (Peterson et al., 1995); *Triaenops rufus* (Hipposideridae), along the Itaranta River (USNM 577064), and near Tolagnaro (Peterson et al., 1995); *Miniopterus majori* (Vespertilionidae), at Manantantely (USNM 577075) and along the Itaranta River

(USNM 577076–577078); and *Mormopterus jugularis* (Molossidae), near Tolagnaro (Peterson et al., 1995). Also, *Pipistrellus nanus* (= *Pipistrellus* sp., *sensu* Peterson et al., 1995) and *Miniopterus (minor) manavi* have been reported from the RNI d’Andohahela (Nicoll & Langrand, 1989).

Discussion

Over the past few years a number of bat inventories have been conducted in the eastern humid forests of Madagascar, and sufficient data are now available to permit preliminary comparisons between the faunas of these different sites. It must be noted that although the data from the RNI d’Andohahela, RNI d’Andringitra, and RS d’Anjanaharibe-Sud are comparable with respect to sampling effort (Goodman, 1996, 1998, herein), the species lists that were generated should not be considered complete. During these surveys no effort was made to employ canopy nets, which are useful for capturing high-flying species, nor were any searches made for roost sites (Voss & Emmons, 1996). Other chiropteran species will undoubtedly be found at these forest sites with further sampling. Even with these limitations, however, several clear patterns have emerged.

On the basis of faunal inventories, the forest-dwelling bat community of the eastern humid forest of Madagascar shows low species richness and little species turnover across nearly the complete length of the island and nearly 12° of latitude (Table 15-2). The majority of bats classified here as forest-dwelling species also occur outside of this habitat, and they presumably forage in open areas.

Probably the most intensive survey of bats in the humid forests of Madagascar was conducted by Pont and Armstrong (1990) in the RNI de Marojejy, where 23 bats of eight species were captured in 8,071 net meter hr. Of this capture effort, 1,063 net meter hr (13% of the total) accrued in primary forest formations where not a single bat was captured. Although this reserve had more intensive sampling effort and higher species richness compared to the other three sites presented in Table 15-2, there are few differences among these four reserves in the forest-dwelling portions of their bat faunas.

Peterson et al. (1995) recognized 29 different bat species on the island. This figure includes species living in open areas, as human commensals, and in humid and dry forests. When compared to other large Old World tropical islands of similar surface area, such as Borneo and New Guinea (Payne et al., 1985; Flannery, 1990) the bat fauna of Madagascar is depauperate. In particular, there is no evidence of a distinct obligate forest-dwelling bat community on Madagascar. The use of harp traps or very fine mesh mist-nets during inventories might reveal a greater diversity of forest-dwelling bats than that demonstrated through the use of standard mist-nets.

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Chapter 16

Carnivora of the Réserve Naturelle Intégrale d'Andohahela, Madagascar

Steven M. Goodman¹ and Mark Pidgeon²

Abstract

The humid forests of parcel 1 of the Réserve Naturelle Intégrale d'Andohahela contain five native (*Galidia elegans*, *Galidictis fasciata*, *Cryptoprocta ferox*, *Eupleres goudotii*, and *Fossa fossana*) and three introduced carnivores (*Canis lupus*, *Felis silvestris*, and *Viverricula indica*). The greatest diversities of native animals were at 440 and 1200 m, with four species each. The known carnivore species of the reserve are identical to those of two other sites in the southern portion of the eastern humid forest. In general, most species of carnivores found in humid forests of Madagascar are known from scattered localities along most of the latitudinal length of this habitat on the island.

Résumé

Les forêts humides de la Parcelle 1 de la Réserve Naturelle Intégrale d'Andohahela renferment cinq carnivores originaires de la région (*Galidia elegans*, *Galidictis fasciata*, *Cryptoprocta ferox*, *Eupleres goudotii*, et *Fossa fossana*) et trois carnivores introduits (*Canis lupus*, *Felis silvestris*, et *Viverricula indica*). La plus grande diversité des animaux indigènes se trouve à 440 m et 1200 m avec quatre espèces. Les espèces de carnivores connues dans la réserve sont identiques à celles trouvées dans deux autres sites dans la partie Sud de la forêt humide de l'Est. En général, la plupart des espèces rencontrées dans les forêts humides de Madagascar sont connues à partir des endroits dispersés le long d'une grande partie de la longueur latitudinale de cet habitat de l'île.

Introduction

Little information is available on the carnivores occurring in the southeastern portion of Madagascar. In his monograph on the carnivores of the island, Albignac (1973) plotted records on distributional maps for only one species south of the Mananara River. Two more recent summaries of the known vertebrate fauna of the Réserve Naturelle Intégrale (RNI)

d'Andohahela listed several species of carnivores (O'Connor et al., 1987; Nicoll & Langrand, 1989); in most cases these records were based not on direct observations but on communications with local forest guards and people living around the reserve. In this chapter we review records of Carnivora in southeastern Madagascar and present information on the carnivores of the RNI d'Andohahela that was gathered during the 1995 expedition at five sites along an elevational gradient in the humid forest of parcel 1 and at a sixth location at 120 m in the spiny forest of parcel 2. We follow the taxonomy of Wozencraft (1993).

¹ Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, IL 60605-2496, U.S.A.

² Route de St. Cergue, 1270 Trélex, Switzerland.

Materials and Methods

Information on the Carnivora of the RNI d'Andohahela was gathered as part of a biological inventory of the reserve (see Chapter 1 for details). In parcel 1 the transect zones were centered at 440, 810, 1200, 1500, and 1875 m. The elevational swath within each zone was ± 75 m from the mid-point. Data on carnivores were gathered using three techniques: direct observations by the survey participants, identification of scats, and systematic trapping.

Within each elevational zone two systems of trap lines were used: one for rodents and the other for carnivores. Rodent lines were baited with peanut butter (see Chapter 14); carnivore lines were baited with rehydrated dried fish, chicken offal, and morsels of fresh river eel. The carnivore lines consisted of 13 National traps placed in the forest, near the camp, off and along trails, and beside rivers. Most of the trapped animals were weighed, checked for reproductive condition, marked, and released near the capture site. Markings consisted of clipping unique patterns of fur from discrete portions of the tail.

Trapped animals saved as voucher specimens were prepared either as flat museum skins, with associated skulls and partial skeletons, or as fluid-preserved carcasses. This material is housed in the Field Museum of Natural History (FMNH), Chicago, and the Département de Biologie Animale, Université d'Antananarivo (UA). Other material reviewed for this paper includes specimens from southeastern Madagascar in the Muséum National d'Histoire Naturelle (MNHN), Paris; National Museum of Natural History (USNM; formerly the United States National Museum), Washington, D.C.; and The Natural History Museum (BMNH; formerly the British Museum of Natural History), London.

Five measurements, in millimeters (mm) or grams (g), were taken for each specimen in the flesh; their abbreviations and definitions are given below.

- TOTL total length of body and tail: from tip of nose to end of last caudal vertebra (not including terminal hair tuft)
- TL tail length: from base of tail (held at right angles to the body) to end of last caudal vertebra (not including terminal hair tuft)
- HFL hind foot length: from heel to tip of longest toe (not including claw)

- EL ear length: from basal notch to distal tip of pinna
- WT weight: measured with Pesola spring scales, to ± 5 g for animals $\leq 1,000$ g and to ± 10 g for those $> 1,000$ g.

Six cranial and four dental dimensions were measured with a digital caliper to the nearest 0.1 mm. These measurements, and their abbreviations, follow.

- BBC breadth of the braincase: greatest distance across the mastoids along an axis perpendicular to the cranium
- CBL condylobasal length: least distance from the posteriormost portions of the occipital condyles to the anteriormost portion of the premaxillae
- CM length of maxillary toothrow: from canine to posteriormost molar
- PL palatal length: from indentation at the posterior edge of the palatine bones to anterior edge of the incisor alveoli
- POB postorbital breadth: least distance across the frontal bones posterior to the postorbital processes
- LTR length of mandibular toothrow: from anterior edge of first incisor to posterior edge of last molar
- ML length of mandible: from mandibular condyle to anteriormost edge of the mandible
- UTR length of maxillary toothrow: from anterior edge of incisors to posterior edge of last molar
- WC width across the upper canines: measured across the base of the canine alveoli
- ZB zygomatic breadth: the greatest distance across the zygomatic arches measured perpendicular to the long axis of the skull

Results

Eight species of carnivores were recorded in the RNI d'Andohahela; five were endemic to the island and three were introduced (Table 16-1). All of these species were recorded in parcel 1. The highest diversity of carnivores was in the 440 m zone, with four native and two introduced species. No native and three introduced carnivores were documented during this inventory in parcel 2.

Three of the five endemic carnivores recorded from the reserve were captured in traps; records

TABLE 16-1. The distribution of carnivores along an elevational gradient in humid forest (parcel 1) and spiny bush (parcel 2) of the RNI d'Andohahela.

Carnivore species	Parcel 1					Parcel 2
	440 m	810 m	1200 m	1500 m	1875 m	120 m
Family Canidae						
<i>Canis lupus*</i>	+					+
Family Felidae						
<i>Felis silvestris*</i>	+					+
Family Herpestidae						
<i>Galidia elegans</i>	+	+	+	+	+	
<i>Galidictis fasciata</i>	+	+	+	+		
Family Viverridae						
<i>Cryptoprocta ferox</i>	+				+	
<i>Eupleres goudotii</i>			+			
<i>Fossa fossana</i>	+	+	+			
<i>Viverricula indica*</i>						+
Total number of species	6	3	4	2	2	3
Total number of endemic species	4	3	4	2	2	0

* Introduced to Madagascar.

of the other two species are based on scats or observations. Trap success with the carnivore lines was generally low and varied from 0.0 to 7.7% (Table 16-2). Quantification of trap success for carnivores captured in the rodent trap lines is presented in Chapter 14. Cranial and external measurements of captured individuals and those preserved as voucher specimens are given in Table 16-3.

Species Accounts

Family Canidae

Canis lupus Linnaeus, 1758

DISTRIBUTION—Domestic dogs were confined to areas in and around human habitation. We found

no clear evidence of feral dogs in habitats deep within the reserve. Our observations of this animal from the RNI d'Andohahela were confined in parcel 1 to the 440 m site, which was close to the forest edge, and in parcel 2 to the 120 m site, not far from several villages (Table 16-1).

COMMENTS—Domestic dogs are regularly used by local people for hunting, principally of *Tenrec ecaudatus* and *Potamochoerus larvatus*, and as guards for cattle and property.

Family Felidae

Felis silvestris Schreber, 1775

DISTRIBUTION—There are records of cats that phenotypically resemble African wild cats from a variety of localities on Madagascar, particularly

TABLE 16-2. Trap capture rates for the carnivore lines established in parcels 1 and 2 of the RNI d'Andohahela.

Descriptive parameter	Parcel 1					Parcel 2
	440 m	810 m	1200 m	1500 m	1875 m	120 m
Cumulative number of trap-nights	91	91	104	104	78	78
Animals captured	1	7	3	4	0	0
Trap-success	1.1%	7.7%	2.9%	3.8%	0.0%	0.0%
Captures of						
<i>Galidia elegans</i>	1	7	1	1	—	—
<i>Galidictis fasciata</i>	—	—	1	3	—	—
<i>Fossa fossana</i>	—	—	1	—	—	—

TABLE 16-3. Measurements of carnivores captured in southeastern Madagascar.

Species	TOTL	TL	HFL	EL	WT
<i>Galidia elegans</i>					
Andohahela adult ♂♂ (n = 4)	629.3 ± 5.5 621-632	262.5 ± 2.9 260-265	70.0 ± 1.7 69-72	30.8 ± 1.3 29-32	846.3 ± 124.0 715-995
Bemangidy adult ♂♂ (n = 2)	574, 601	237, 258	74, 75	30, 30	
Bemangidy adult ♀ (n = 1)	568	236	73	29	
Bemangidy subadult ♀ (n = 1)	498	218	67	28	
<i>Galidictis fasciata</i>					
adult ♂ (n = 1)	632	293	73	31	745
adult ♀ (n = 1)	559	249	69	32	585
subadult ♀ (n = 1)	573	236	65	31	385
<i>Fossa fossana</i>					
adult ♂ (n = 1)	630	221	84	44	1,050
adult ♀♀ (n = 2)	698, 698	229, 264	92, 93	45, 48	—
combined	675.3 ± 39.2 630-698	238.0 ± 22.9 221-264	89.7 ± 4.9 84-93	45.7 ± 2.1 44-48	
<i>Viverricula indica</i> ♀ (n = 1)	751	325	81	38	

TABLE 16-3. Continued.

	CBL	ZB	POB	BBC	WC	PL	UTR	CM	ML	LTR
<i>Galidia elegans</i>										
Andohahela adult	69.6 ± 1.7	39.3 ± 0.9	12.4 ± 0.9	28.9 ± 0.6	13.8 ± 0.3	32.1 ± 0.5	29.6 ± 0.6	24.1 ± 0.6	42.3 ± 0.8	28.8 ± 0.5
♂♂ (n = 4)	67.1-71.1	38.5-40.4	11.8-13.7	28.2-29.7	13.4-14.2	31.5-32.7	29.0-30.4	23.4-24.9	41.5-43.4	28.2-29.5
Bemangidy adult ♂♂	67.2	38.9	11.8	28.3	13.1	30.7	29.9	23.6	41.4	27.8
	69.6	41.0	12.8	28.7	14.1	31.1				
<i>Galidictis fasciata</i>										
adult ♂ (n = 1)	69.6	40.5	13.6	29.5	16.1	32.2	29.4	23.8	44.5	28.1
adult ♀ (n = 1)	67.7	37.0	12.3	27.9	14.3	30.8	28.7	23.5	42.9	27.6
subadult ♀ (n = 1)	62.1	35.1	14.1	28.5	12.0	28.3	26.4	21.5	37.7	26.3
<i>Fossa fossana</i>										
adult ♂ (n = 1)	88.3	43.7	14.5	34.0	12.6	46.9	46.8	—	61.0	46.7
adult ♀ (n = 1)	98.6	45.6	11.7	32.3	14.1	53.6	50.5	43.2	69.1	49.5

Specimens include: *Galidia elegans*—FMNH 85192-85194, 85873, 156649-156651; *Galidictis fasciata*—FMNH 156549, 156652, 156653; *Fossa fossana*—FMNH 85195, 85196, 156648; and *Viverricula indica*—FMNH 85201.

Data are presented as mean ± standard deviation, range, and number of specimens (in parentheses). Units are millimeters (mm) for all measurements except WT (weight), which is in grams (g). Abbreviations are explained on p. 260 of the text. For cases in which two or fewer specimens were available, the measurements themselves are presented.

western deciduous forest and southern spiny bush (M. Nicoll, pers. comm.). In several cases it is unclear whether these individuals represent feral domestic cats or a remnant population of introduced African wild cats. All of our records of this species in the RNI d'Andohahela are from the forest edge or outside the forest at 440 m in parcel 1 and 120 m in parcel 2 (Table 16-1). Reports of wild cats in the region date from at least the latter half of the 17th century (Flacourt, 1658).

Family Herpestidae
Subfamily Galidiinae

***Galidia elegans elegans* I. Geoffroy Saint-Hilaire, 1837**

DISTRIBUTION—*Galidia elegans* is one of the most broadly distributed native carnivores on Madagascar, occurring throughout the length of the eastern humid forest from Tolagnaro to Montagne d'Ambre, as well as in the Sambirano and western forests (Albignac, 1973; O'Connor et al., 1987). It was the most commonly observed and captured carnivore in parcel 1 of the RNI d'Andohahela. This species was recorded over the complete altitudinal breadth of the transect from 440 to 1875 m (Table 16-1). It was not found in parcel 2 of the reserve, but Tandroy villagers have reported occasional sightings of *Galidia* in the spiny bush during the short wet season (T. Saotsy, pers. comm.).

ECOLOGY AND REPRODUCTION—*Galidia elegans* was often observed in and around our camps and was attracted to the sounds and smells of the kitchen and laboratory areas. Trap captures and sight records showed it to be most common in the 810 m zone, where seven individuals were captured in 91 trap-nights (7.7%) in the carnivore lines (Table 16-2). This species was also captured in all other elevational zones (except 1875 m) in National traps set for rodents and baited with peanut butter (see Chapter 14).

An individual that was captured, marked, and released in the 810 m zone was observed several days later in the 1200 m zone. There was a straight line displacement of approximately 2.5 km between the two sites. Nine of the 10 *Galidia* captured in the carnivore lines were males, and about half of them had scrotal testes.

The large number of *Galidia elegans* trapped and observed during the survey certainly reflects a high overall local abundance. It is presumably

the most common carnivore in the reserve. The more frequent sightings of *Galidia* compared to other carnivore species are largely due to its bold and inquisitive nature; certainly they reflect its abundance, diurnal activity, and utilization of trails and river margins. Another contributory factor may thus be that our camps were always close to water. On several occasions this species was observed moving through the mid-canopy, up to 10 m off the ground, and passing between large canopy trees via touching limbs. Arboreal behavior was previously reported for this species (Rand, 1935; Goodman, 1996). When moving about arboreally, a *G. elegans* would often tear open clumps of epiphytes clinging to tree branches or stick its head into small crevices or holes. Although no observations were made of food items being taken, this may be how the carnivore finds and feeds on the small nocturnal primates (*Microcebus* and *Cheirogaleus*) that it is known to prey upon (Goodman et al., 1993; Wright & Martin, 1995). This carnivore was also observed being mobbed by two species of birds, *Phyllastrephus zosterops* and *Xenopirostris polleni* (F. Hawkins, in litt.). On one occasion *G. elegans* was observed hunting at the edge of a stream and diving into the water in pursuit of amphibian prey (A. Rase-limanana, pers. comm.).

COMMENTS—Currently three subspecies of *Galidia elegans* are recognized, with the nominate form occurring from Tolagnaro north to at least the Antalaha region (Albignac, 1973). On the basis of specimens captured in the RNI d'Andohahela and comparison to material housed in museums from the eastern humid forests, the population living in and around the reserve shows noticeable differences in pelage coloration from typical *G. e. elegans*. The red pelage is often much darker and more saturated with a deep rufous-red color than more northerly populations of *G. e. elegans*. Further, the ventrum of most individuals from the reserve is distinctly black, and this color often extends down the inner surface of the hind and forelegs and anteriorly to the chin. It is not yet clear whether this variation in pelage coloration is correlated with mensural or osteological differences from other eastern humid forest populations or is part of a broad latitudinal cline. The form occurring in the dry deciduous forest of the west, *G. e. occidentalis* Albignac, 1971, apparently shares some pelage characters with the Andohahela populations.

SPECIMENS EXAMINED—Parcel 1, 12.5 km NW of Eminiminy, 24°35.6'S, 46°44.3'E, 810 m

(FMNH 156649, 156651); parcel 1, 15.0 km NW of Eminiminy, 24°34.2'S, 46°43.9'E, 1500 m (FMNH 156650); Bemangidy, approximately 72 km N of Tolagnaro, 24°34'S, 47°14'E (FMNH 85192–85194, 85873).

Galidictis fasciata fasciata (Gmelin, 1788)

DISTRIBUTION—In the RNI d'Andohahela *Galidictis fasciata* was observed or captured in the 440, 810, 1200, and 1500 m zones. There are widely scattered records of this species in the central portion of the eastern humid forest from the RNI de Zahamena south to the region between Farafangana and Manakara (N. Rakotoarison, pers. comm.; Albignac, 1973). The previous southernmost record appears to be Vondrozo (BMNH 1935.01.08.305, MNHN 1932-3539). Our records from the RNI d'Andohahela extend the distribution of *G. fasciata* about 250 km further south.

ECOLOGY AND REPRODUCTION—This carnivore was occasionally seen at night on trails within the forest and in and around our camps. An adult female and a young female were taken in the same trap set on consecutive days. The trap site was on the ground in a passageway under a fallen and rotten log. This species was trapped nearly as often as it was seen, almost certainly because of its secretive nocturnal behavior.

The four individuals captured included an adult male, two adult females, and a subadult female. The adult female had a single pair of small inguinal mammae, and the adult male had scrotal testes measuring 25 × 12 mm with slightly convoluted epididymides. The subadult female showed no signs of reproductive activity.

COMMENTS—Trapping showed *Galidictis fasciata* to be most common in the 1500 m zone. Although it is difficult to compare relative densities of carnivores along our elevational transect, *G. fasciata* seems to be the second most common species of carnivore in parcel 1 of the RNI d'Andohahela. It occurs from lowland to montane forest. *Galidictis f. fasciata* is the subspecies found in the southern portion of the eastern humid forest (Albignac, 1973, p. 46, *contra* fig. 5). The local Tanosy people living near the eastern border of parcel 1 call this species *vontsira fotsy*.

SPECIMENS EXAMINED—Parcel 1, 13.5 km NW of Eminiminy, 24°35.0'S, 46°44.1'E, 1200 m (FMNH 156652); parcel 1, 15.0 km NW of Em-

iniminy, 24°34.2'S, 46°43.9'E, 1500 m (FMNH 156549, 156653).

Family Viverridae
Subfamily Cryptoproctinae

Cryptoprocta ferox Bennett, 1833

DISTRIBUTION—We found evidence of *Cryptoprocta ferox* at two sites in the RNI d'Andohahela. Scats identifiable to this species were found on the trail below the 440 m camp, at 1850 m at the base of the hump of Pic Trafonaomby, and at about 1800 m in an open area by a water hole. This species has a broad distribution across much of Madagascar, in and near natural forested habitats from sea level to high mountain zones above the forest line (Albignac, 1973; Goodman et al., 1997). Previous records of *C. ferox* from the RNI d'Andohahela include reports from forest guardians or local villagers for parcels 1 and 2 (O'Connor et al., 1987). People living in rural areas near forested areas know this animal well and note that it occasionally feeds on village chickens.

COMMENTS—The scat found near the 440 m camp contained fur remains of *Haplemur griseus*. *Cryptoprocta* has been reported feeding on a wide variety of lemur species (Goodman et al., 1993; Rasoloarison et al. 1995; Goodman et al., 1997; Wright et al., 1997); but as far as we can determine this is the first evidence of it preying on *H. griseus*. The scat from the base of Trafonaomby held bones of at least two *Oryzorictes hova*, one *Microgale thomasi*, and two *M. cowani*. All of these lipotyphlans were trapped in the 1875 m zone and weighed less than 35 g (see Chapter 13). *Cryptoprocta* living in other high mountain zones show a dramatic drop in mean body size of prey in comparison to those in lower lying areas of forest (Goodman et al., 1997).

Subfamily Euplerinae

Eupleres goudotii Doyère, 1835

DISTRIBUTION—*Eupleres goudotii* was seen once during the 1995 inventory of the RNI d'Andohahela. On 15 November a single individual was observed by F Hawkins in the 1200 m zone. The animal was moving through a valley bottom at 1615 hr.

The distribution of *Eupleres goudotii* is poorly known, but it has been recorded from scattered localities in the eastern humid forest from Montagne d'Ambre (Albignac, 1973; Nicoll & Langrand, 1989) south to the RNI d'Andringitra (Goodman, 1996). It has also been reported in dry forest from the Sambirano south to Baly (Albignac, 1973; Hawkins, 1994).

Fossa fossana (Müller, 1776)

DISTRIBUTION—This species was recorded during the 1995 inventory of the RNI d'Andohahela in the 440, 810, and 1200 m zones. It has been reported from numerous localities in the eastern humid forest from the Antalaha area south to the RNI d'Andringitra and Réserve Spéciale (RS) du Pic d'Ivohibe (Albignac, 1973; Goodman, 1996), as well as near Vondrozo (Rand, 1935). Forest guardians and local villagers living near parcel 1 of the RNI d'Andohahela noted the presence of this species in the reserve (O'Connor et al., 1987). We have also observed this species in the littoral forest near Manafiafy.

ECOLOGY AND REPRODUCTION—The single individual captured was a subadult male with slightly scrotal testes measuring 5×3 mm and non-convoluted epididymides. The animal was in the process of replacing the deciduous upper incisors with permanent teeth. All other records of this species in the RNI d'Andohahela were observations made at night. At least twice this species was observed pilfering food stocks in our camps during the night.

COMMENTS—In November 1948 Harry Hoogstraal collected three *Fossa fossana* in the vicinity of Bemangidy. We examined and measured two of these specimens (Table 16-3). Inscriptions on the specimen labels indicate that one was "trapped with meat bait at edge of original forest" and another "was trapped with fruit bait beside stream at edge of original forest."

SPECIMENS EXAMINED—Parcel 1, 13.5 km NW of Eminiminy, $24^{\circ}35.0'S$, $46^{\circ}44.1'E$, 1200 m (FMNH 156648); Bemangidy, approximately 72 km N of Tolagnaro, $24^{\circ}34'S$, $47^{\circ}14'E$ (FMNH 85195, 85196; USNM 318107).

Subfamily Viverrinae

Viverricula indica (Desmarest, 1804)

DISTRIBUTION—This introduced species has been previously reported from parcel 3 of the RNI

d'Andohahela (O'Connor et al., 1987); we found it only in parcel 2 during the 1995 mission. *Viverricula indica* is broadly distributed across many areas of the island, particularly in close proximity to rural settlements. It is found in a variety of environments from the suburbs of Antananarivo to lowland agricultural areas, humid forest, and spiny bush habitat. We commonly observed this species in the littoral forests near Manafiafy.

COMMENTS—In December 1948 Harry Hoogstraal collected a specimen of *Viverricula indica* near Bemangidy that, based on notes inscribed on the label, was "trapped in manioc field [with] fish bait."

SPECIMENS EXAMINED—Bemangidy, approximately 72 km N of Tolagnaro, $24^{\circ}34'S$, $47^{\circ}14'E$ (FMNH 85201).

Discussion

The only carnivore species previously reported from the reserve but not documented during the 1995 inventory is *Salanoia concolor*. (I. Geoffroy Saint-Hilaire, 1837) (O'Connor et al., 1987), a poorly known animal that is apparently confined to humid forest (Albignac, 1973). The report of *S. concolor* in the RNI d'Andohahela was based on information from a person living close to parcel 1. This species is rather nondescript and may have been confused with another species of carnivore, notably *Galidia elegans*. The presence of *S. concolor* in the reserve thus needs confirmation. The southernmost documented record of *S. concolor* is from the Périnet area (Albignac, 1973).

Five of the eight carnivore species known from parcel 1 of the RNI d'Andohahela are endemic to Madagascar, and the other three are introduced. A comparison of sites in the eastern humid forest that have been relatively well surveyed for carnivores shows a similar fauna across a broad latitudinal area (Table 16-4). The sites of RNI d'Andohahela, RNI d'Andringitra, and the Parc National (PN) de Ranomafana have identical native carnivore faunas. The Réserve de Biosphère (RB) de Mananara has the same native carnivore faunas as these other three sites, with the addition of *Salanoia concolor*.

No native carnivore was recorded in parcel 2 of the RNI d'Andohahela during the 1995 inventory, but there is a report of *Cryptoprocta ferox*

TABLE 16-4. The known distribution of native carnivores at several sites in the eastern humid forests of Madagascar.

Species	Latitude: Source of information*:	RNI d'Andohahela 24°S 1	RNI d'Andringitra 22°S 2	PN de Ranomafana 21°S 3	RB de Mananara 16°S 4
<i>Galidia elegans</i>		+	+	+	+
<i>Galidictis fasciata</i>		+	+	+	+
<i>Salanoia concolor</i>		—	—	—	+
<i>Cryptoprocta ferox</i>		+	+	+	+
<i>Eupleres goudotii</i>		+	+	+	+
<i>Fossa fossana</i>		+	+	+	+
Total number of endemic species		5	5	5	6

* 1 = this study; 2 = Goodman (1996); 3 = Nicoll and Langrand (1989) and P. Wright (pers. comm.); 4 = Nicoll and Langrand (1989).

occurring there (O'Connor et al., 1987), and there have been local sightings of *Galidia elegans* (T. Saotsoy, pers. comm.). On the basis of current distributional information, no other species of Malagasy carnivore would be expected to occur in this parcel. *Cryptoprocta* is the only native carnivore that occurs in both parcels 1 and 2. These two sites are separated by an air distance of about 20 km. Three species of introduced carnivores were recorded in parcel 2; two of these are human commensals and may occasionally revert to being feral (*Canis lupus* and *Felis silvestris*), and the third lives completely in a feral state (*Viverricula indica*). There is little evidence that introduced carnivores are able to penetrate far into humid forest habitat, and these animals do not pose any apparent threat to the native carnivore populations.

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Chapter 17

Lemurs of the Réserve Naturelle Intégrale d'Andohahela, Madagascar

Anna T. C. Feistner¹ and Jutta Schmid²

Abstract

An inventory of the lemur fauna of the Réserve Naturelle Intégrale d'Andohahela was conducted between 18 October and 16 December 1995. Study sites in parcel 1 of the reserve were located at five different elevations, 440, 810, 1200, 1500, and 1875 m, up an altitudinal gradient in humid forest. In addition, one site was located at 120 m elevation within the spiny forest portion of the reserve (parcel 2). At each site the presence and relative abundance of lemur species were estimated using the line transect method. A total of eight lemur taxa were recorded in parcel 1 (*Propithecus verreauxi verreauxi*, *Eulemur fulvus collaris*, *Hapalemur griseus*, *Microcebus rufus*, *Cheirogaleus major*, *Avahi laniger*, *Lepilemur mustelinus*, and *Daubentonia madagascariensis*). Species richness (eight species) was highest at the lowest elevation (440 m) and decreased to a relatively constant level (four to six species) for the four higher elevational zones. The single observed group of *P. v. verreauxi*, which is generally a species of the dry deciduous forest and spiny thorn scrub, contained some individuals of the dark (*P. v. 'majori'*) morph. Distinctive signs of feeding by *Daubentonia* were recorded at every elevational level. Four species of lemurs were sighted in the spiny forest (*P. v. verreauxi*, *Lemur catta*, *Microcebus murinus*, and *Lepilemur leucopus*). A fifth species, *Phaner furcifer* ssp., was recorded by vocalizations only. In both wet and dry forest parcels, further efforts are necessary to ensure long-term protection of the RNI d'Andohahela and prevent the degradation of its fauna and flora. There was evidence that *E. f. collaris* is hunted within the reserve, although the RNI d'Andohahela is the only protected area in Madagascar where this taxon occurs naturally.

Résumé

Un inventaire des lémuriers de la Réserve Naturelle Intégrale d'Andohahela a été effectué entre le 18 octobre et 16 décembre 1995. Les sites d'études sont situés à cinq différentes altitudes, 440 m, 810 m, 1200 m, 1500 m et 1875 m, le long de la pente Est de la Parcelle 1 de la Réserve, une forêt humide de 63.000 ha. En outre, un site est situé à une altitude de 120 m dans une forêt épineuse de 12.920 ha de la Parcelle 2. Dans chaque site, une présence et une abondance relative d'espèces de lémuriers ont été estimées en utilisant la méthode de transect linéaire. Un total de 8 taxa de lémuriers est inventorié dans la forêt humide (*Propithecus verreauxi verreauxi*, *Eulemur fulvus collaris*, *Hapalemur griseus*, *Microcebus rufus*, *Cheirogaleus major*, *Avahi laniger*, *Lepilemur mustelinus*, et *Daubentonia madagascariensis*). La zone la plus riche en espèces se trouve à la plus basse altitude (440 m). Cette richesse

¹ Jersey Wildlife Preservation Trust, Les Augrès Manor, Trinity, Jersey JE3 58P, Channel Islands.

² Deutsches Primatenzentrum, Kellnerweg 4, 37077 Göttingen, Germany, and Abteilung für Verhaltenphysiologie, Beim Kupferhammer 8, 72070 Tübingen, Germany.

diminue mais ensuite reste constante pour les quatre zones de niveau supérieur. Le seul groupe de *Propithecus verreauxi verreauxi*, généralement une espèce rencontrée en forêt sèche et broussailles épineuses, contient quelques individus de couleur foncée ('*majori*'). Des signes distinctifs d'alimentation par *Daubentonia* sont inventoriés à chaque niveau altitudinal de la forêt humide. Dans la forêt épineuse, on a distingué quatre espèces de lémuriens (*P. v. verreauxi*, *Lemur catta*, *Microcebus murinus*, et *Lepilemur leucopus*). Une cinquième espèce, *Phaner furcifer* ssp., a été inventoriée par vocalisations seulement. Dans les Parcelles de forêt humide et sèche, des efforts supplémentaires doivent être déployés afin d'assurer une protection à long terme de la Réserve et empêcher la dégradation de sa faune et de sa flore. On a décelé des preuves de chasse de *E. f. collaris* à l'intérieur de la Réserve, pourtant la RNI d'Andohahela est la seule aire protégée à Madagascar où le taxon apparaît d'une manière naturelle.

Introduction

Madagascar has been isolated from other land masses for some 88 million years; consequently its flora and fauna have evolved in isolation (Storey et al., 1995). Endemism is extremely high. Madagascar is considered one of the world's major "hotspots" of biodiversity (Myers, 1988, 1990). One of the major adaptive radiations in Madagascar is among the primates. The primate fauna is highly diverse (comprising about 32 species) and entirely endemic (the lemurs found on the Comoro Islands almost certainly were introduced). Madagascar is also a high priority for conservation efforts because many of its unique environments are under threat.

The primate fauna is restricted to forest zones (eastern humid forests, western dry forests, and southern spiny forests). These forests are disappearing as land is cleared for agricultural purposes, as trees are felled to provide building materials and charcoal, and as a result of commercial logging. Moreover, some lemurs are also hunted for food.

In order to develop effective conservation strategies for the unique habitats in Madagascar, information on the distribution and abundance of their faunas and floras is crucial. Madagascar already has a system of protected areas, but accurate inventories and effective protection are lacking for many of the reserves.

As part of a program to assess biodiversity within the protected areas of Madagascar, international teams of scientists have been undertaking floral and faunal inventories in a variety of humid and dry forest sites (Goodman & Langrand, 1994; Goodman, 1996; Langrand & Goodman, 1997; Goodman, 1998). These surveys not only provide information important for conservation planning, but they also help in developing an understanding

of patterns of diversity and variation with latitude, relief, and elevation.

The work reported here was carried out in the Réserve Naturelle Intégrale (RNI) d'Andohahela. This reserve is of particular interest and importance because it includes the southernmost tropical humid forests in the Old World, traverses the east-west divide in Madagascar, and encompasses areas of dry spiny forest. The scant information on lemur diversity and density in the RNI d'Andohahela is inconsistent (Nicoll & Langrand, 1989; Mittermeier et al., 1992, 1994) in that the published primate species lists contain different species (see especially Mittermeier et al., 1992, 1994). The reserve is known to be important for at least one lemur, the Collared Brown Lemur *Eulemur fulvus collaris*, because it represents the only protected area in which this taxon occurs (but see Sterling & Ramarason, 1996).

The aim of our work on lemurs was to assess the diversity and abundance of that fauna in the RNI d'Andohahela. Most of our effort was concentrated in the eastern humid forest (parcel 1), where assessments were undertaken at a variety of elevations on the eastern slopes of the Andohahela Massif. To complete the primate inventory, assessments were also undertaken in the dry western spiny forest (parcel 2).

Materials and Methods

In order to enhance the validity of comparisons between different protected areas, methods for rapid assessment of the primate fauna were standardized across forest sites. The methods used in the RNI d'Andohahela were the same as those used in the RNI d'Andringitra (Sterling & Ramarason, 1996), the Réserve Spéciale (RS)

TABLE 17-1. Description of the different habitat types found along the trails walked during censuses at each site in the RNI d'Andohahela. Trails at 440–1875 m were located in the humid forest of parcel 1; those at 120 m were in the spiny forest of parcel 2.

Trail	Trail length (m)	General habitat characteristics
440a	1200	Open forest with a high proportion of lianas (canopy 11–15 m); slope: dense steep forest (canopy 8–12 m)
440b	1150	Open forest with dense lianas; slope: forest (canopy 10–12 m); open ridge forest, (degraded) riverine forest
810a	1750	Riverine forest: dense ground vegetation, bamboo, tree ferns (canopy 5–6 m); open forest (canopy 12–15 m)
810b	600	Slope: steep forest (canopy 8–10 m); ridge: open forest (canopy 15–20 m), bamboo and grassy bamboo; rocks on one side; slope: riverine forest
1200a	950	Open forest; no ground vegetation (canopy 12–15 m); ridge: mossy forest (canopy 8–10 m), bamboo, tree ferns (canopy 8 m); slope: steep and humid forest (canopy 6 m)
1200b	1000	Open forest (canopy 10–12 m); ground vegetation, leaf litter, liana; slope: rocks, open forest; valley: open riverine forest, grassy bamboo
1500a	1200	Ridge: open forest (canopy 6–8 m), no ground vegetation; bamboo and grassy bamboo
1500b	725	Slope: steep and open forest (canopy 10 m); ridge: grassy bamboo, mossy, few trees (canopy 4–5 m)
1500c	365	Ridge: open forest (canopy 8–10 m), thick ground vegetation; tree ferns (canopy 8 m)
1875a	190	Ridge: mountain forest (canopy 2–4 m), mossy, ground vegetation 30–50 cm, rocky, moss, sedge
1875b	810	Ridge: moss forest (canopy 4–8 m), rocky, lianas
1875c	690	Ridge: moss and bamboo forest, sedge plateau
120a	3500	Main road: degraded spiny forest (canopy 2–3 m), sisal patches; streamside: spiny and gallery forest with baobabs (canopy 5–10 m)
120b	3000	Slope: spiny forest; ridge: spiny forest (canopy 2–3 m); main road: patchy spiny forest, degraded
120c	900	Degraded spiny forest

d'Anjanaharibe-Sud (Schmid & Smolker, 1998), and on the Masoala Peninsula (Sterling & Rakotoarison, 1998).

Study Sites

Censuses for lemurs were conducted at five elevations in the humid forest along the eastern slope of the Andohahela Massif (parcel 1) between 18 October and 5 December 1995. In addition, an inventory of lemur species was undertaken at one site in the spiny forest of parcel 2 of the same reserve between 8 and 14 December 1995. The team, consisting of two researchers experienced in observing Malagasy primates, visited each of the six sites for a minimum of 7 days.

Survey sites of parcel 1 were located at five different elevations. All transects were within 75 m elevation above or below sites centered at 440, 810, 1200, and 1500 m. Due to the lack of water, the fifth camp site was located at 1710 m but the

transect zone was centered at 1875 m. The sixth site, in the spiny forest of parcel 2, was located east of Hazofotsy at an altitude of 120 m (see Chapter 1).

The line transect method was employed (National Research Council, 1981). At each location two or three trails of varying lengths (humid forest: 190–1750 m; spiny forest: 900–4000 m) were used for lemur surveys. We utilized preexisting trails left by bush pigs, cows, and people, as well as newly cut trails. We attempted to select trails that covered a variety of forest habitats, including ridges, slopes, valleys, and stream/river courses. A general description of the forest type along each trail is given in Table 17-1. Each trail was marked in 20 or 25 m cumulative intervals with flagging tape.

Two researchers walked either singly or in tandem slowly (ca. 0.6 km/hr) along the trails to census lemurs. Diurnal censuses took place at times of increased lemur activity, in the morning (0600–1130 hr) and in the afternoon (1500–1730 hr).

Walks were always separated by a time interval of at least 6 hr when trails were censused twice per day during daylight hours. For nocturnal samples, trails were walked after dark, between 1830 and 2230 hr. Whenever possible, trails were walked from the direction opposite that of the previous sample to reduce potential biases (Brockelman & Ali, 1987). When the terrain was difficult, we paused fairly regularly (approximately every 25 m) to watch and listen for signs of primate presence, such as vocalizations or movements in the vegetation. At night the dim light of a headlamp was used to pick up the eyeshine from the reflective tapetum lucidum of nocturnal lemurs. Once detected, a more powerful handheld flashlight and binoculars (7 × 40) were used for species identification.

For all observations we noted the species, time of contact, position on the transect, elevation, distance from the observer, angle, height from the ground, and habitat type. The perpendicular distance from the trail was estimated for the first individual seen in each group. Whenever possible, we also recorded the number of individuals, age/sex composition, and general behavior. No more than 10 min were spent for any single sighting. In the humid forest, censusing along each transect was repeated three to four times (except trail 1875c) for nocturnal transects and nine to thirteen times (cf. trail 1875c) for diurnal transects. In the spiny forest, trails were censused one to three times at night and three to nine times in daylight. We did not conduct census walks when the viewing distance was restricted to less than 15 m, as was sometimes the case owing to dense fog or heavy rain.

Inadequate sample sizes, such as the few repetitions of each transect and the relatively short distances covered at each site, prevented us from determining density values (Whitesides et al., 1988; Ganzhorn, 1992, 1994; Sterling & Ramarson, 1996; Schmid & Smolker, 1998). The mean numbers of lemur sightings per km transect were calculated, however. In addition, the mean detection distance, perpendicular to the trail, at which lemurs were seen was compiled for each species and trail. For each species where we did not find statistically significant differences across trails per site, a single average detection distance was calculated. For diurnal censuses the mean number of groups and for nocturnal censuses the mean number of individuals observed within the transects were determined. Lemurs heard but not seen during census walks or those seen outside census

walks by us or other researchers were not included in calculations of encounter rate for either diurnal or nocturnal surveys. Species accumulation curves were based on sightings and vocalizations during transect walks.

Additional Observations

Apart from the systematic transect surveys, other general observations were made during the day. Within each elevational zone we explored the forest away from the trail system used for transects to look for secondary signs of the presence of certain primates. These included characteristic feeding signs of *Daubentonia madagascariensis* (gnaw marks from excavation of dead wood, living branches, or bamboo) or sleeping sites for nocturnal species (e.g., nests for *Daubentonia* or tree holes for *Cheirogaleus* or *Microcebus*).

Within the 1875 m zone there were many signs of *Daubentonia* feeding on bamboo stems. We therefore decided to investigate the stems to see if we could locate their potential prey. A bamboo stem was cut less than 30 cm above the ground. Each segment of the stem, until it became very thin and leaves sprouted, was opened, and the contents, if any, were examined. Any invertebrates contained within the stem were collected and preserved in alcohol. In two areas located approximately 60 m and 120 m from trail 1875a, respectively, a total of 25 intact bamboo stems (5 m apart), ranging in length from 2.5 to 6.0 m, were examined. In total, 333 segments were opened.

Results

Species Accumulation Curves

Species accumulation curves are shown in Figure 17-1. For nocturnal censuses at the survey sites in the humid forest of the RNI d'Andohahela, no additional species were recorded in the 440 and 810 m zones after 3 hr of observation (Fig. 17-1a,b). In the 1500 and 1875 m zones all lemurs were recorded after only 2 hr of observation (Fig. 17-1d,e), whereas at 1200 m all nocturnal lemurs were recorded after 1 hr of census walks (Fig. 17-1c). The species accumulation curve for diurnal lemurs was much more variable. At 440 m the curve did not plateau until 30 hr of

observation (Fig. 17-1a). This was due to the unexpected sighting of *Propithecus v. verreauxi* that occurred on the last day of censusing. At 810 m all diurnal lemurs were encountered within 2 hr, whereas at 1200 m 12 hr were required (Fig. 17-1b, c). At 1500 m only 2 hr were needed, but at the highest elevation (1875 m) 9 hr of censusing was necessary before all species were recorded (Fig. 17-1d,e).

At the survey site in the spiny forest, the species accumulation curve for lemurs recorded during nocturnal censuses reached its plateau after only 1 hr of observation (Fig. 17-1f). For diurnal censuses, we recorded two species after 4 hr of censusing, and although walks for day censusing totaled 52 hr, no additional species were seen (Fig. 17-1f).

Species Diversity

In total, one diurnal species (*Propithecus verreauxi verreauxi*), two cathemeral species (*Eulemur fulvus collaris* and *Hapalemur griseus*), and five typically nocturnal species (*Microcebus rufus*, *Cheirogaleus major*, *Avahi laniger*, *Lepilemur mustelinus*, and *Daubentonia madagascariensis*) were found in five elevational zones of parcel 1 of the RNI d'Andohahela (Table 17-2). All taxa were directly observed except for *Daubentonia*, which was recorded indirectly by from its characteristic feeding signs (Duckworth, 1993; Erickson, 1995). Species diversity was highest in the 440 m zone, where all eight lemur species recorded in parcel 1 were found. Five lemur species were present in the 810 and 1200 m zones, six species in the 1500 m zone, and only four in the 1875 m zone. *Eulemur f. collaris*, *M. rufus*, *C. major*, and *D. madagascariensis* were found at all elevations. *Hapalemur griseus* was absent from the highest elevational zone. *Avahi laniger* was seen in the 440 m and 1500 m zones, and *L. mustelinus* was only present at 440 m. *Propithecus v. verreauxi* is generally considered a dry forest species, and our single record of it at 440 m was exceptional. The lengths of transects, numbers of census walks, and species recorded in the various elevational zones of parcel 1 are listed in Table 17-3 for nocturnal censuses and in Table 17-4 for diurnal censuses. In total, we walked 39.2 km during nocturnal censuses and 117.2 km during diurnal censuses.

Five lemur species were recorded in the spiny forest of parcel 2 of the RNI d'Andohahela; two

of these were diurnal (*Propithecus verreauxi verreauxi* and *Lemur catta*) and three were nocturnal (*Microcebus murinus*, *Lepilemur leucopus*, and *Phaner furcifer* ssp.) (Table 17-2). Sleeping *P. v. verreauxi* were occasionally encountered during nocturnal censuses. *Propithecus v. verreauxi*, *M. rufus*, and *L. mustelinus* were observed directly. *Lemur catta* was identified from vocalizations heard during the transect walks, although a group was encountered during general observations. *Phaner furcifer* ssp. was identified only from vocalizations. Table 17-5 lists the lengths of transects, numbers of census walks, and observed species for night and day censuses in the spiny forest. During night surveys a total of 18.9 km was walked, with 65.7 km walked during the day surveys.

Species Descriptions

Pelage and morphological characteristics as well as reports on activity or social behavior were derived for the lemurs from both systematic and general field observations. Sexual differences in the morphological characters are restricted to diurnal species. Any observations related to breeding activity are also included under the species descriptions.

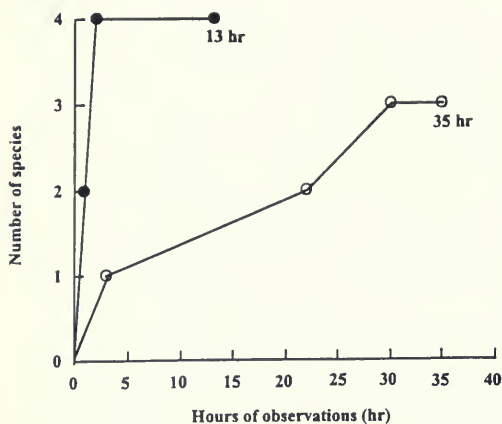
Microcebus rufus (Rufous Mouse Lemur)

Microcebus rufus was found at all altitudes in the humid forest. The mean encounter rate remained approximately constant across the elevational range from 440 to 1500 m (Table 17-3), but it dropped off at 1875 m, where there were only two sightings for 4.5 km of trail walked. The mouse lemurs had relatively small ears; they were brown to rufous on the dorsum and whitish on the ventrum. The head was reddish in color and the nose was not very prominent. *Microcebus rufus* were almost always seen singly and were very active, with rapid movements. They were generally found in dense bushy vegetation, as well as in the taller trees of the forest.

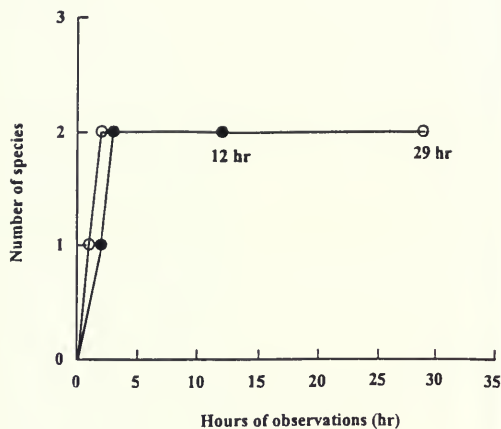
Microcebus murinus (Grey Mouse Lemur)

Census results showed that *Microcebus murinus* was the most common nocturnal lemur spe-

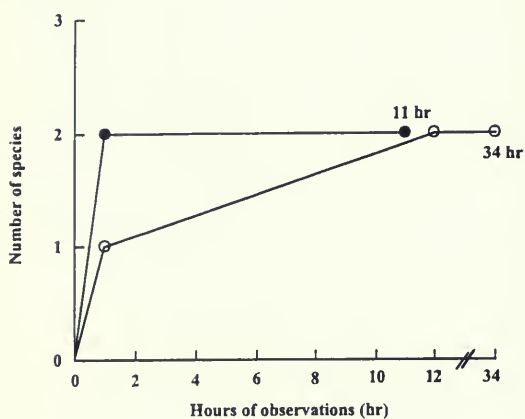
A) 440 m



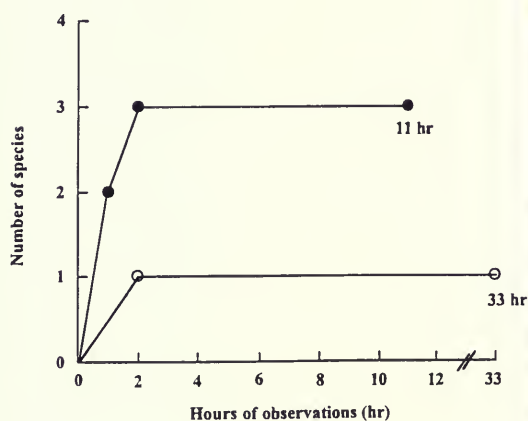
B) 810 m



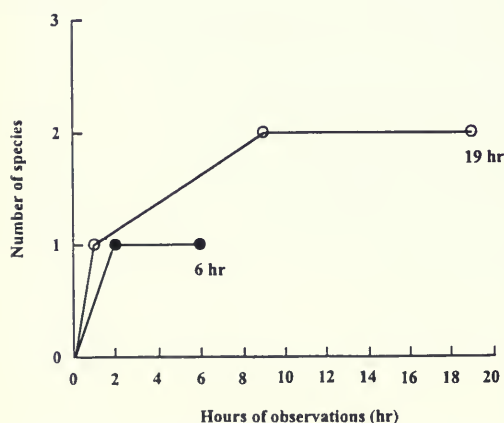
C) 1200 m



D) 1500 m



E) 1875 m



F) 120 m

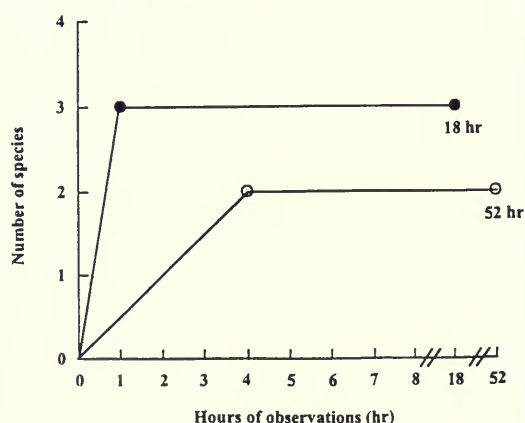


FIG. 17-1. Species accumulation curves as a function of observation hours for nocturnal (●) and diurnal (○) lemur species censused in the RNI d'Andohahela. Humid forest at 440 m (A), 810 m (B), 1200 m (C), 1500 m (D), and 1800 m (E) elevation zones, spiny forest at 120 m (F).

TABLE 17-2. The primate species found in the humid forest (parcel 1) and spiny bush (parcel 2) of RNI d'Andohahela listed by elevational zone. Species were recorded during survey walks or during additional observations.

Species	Parcel 1					Parcel 2
	440 m	810 m	1200 m	1500 m	1875 m	120 m
<i>Microcebus rufus</i>	+	+	+	+	+	
<i>Microcebus murinus</i>						+
<i>Cheirogaleus major</i>	+	+	+	+	+	
<i>Phaner furcifer</i> ssp.						+
<i>Avahi laniger</i>	+			+		
<i>Lepilemur mustelinus</i>	+					
<i>Lepilemur leucopus</i>						+
<i>Daubentonia madagascariensis</i>	fd	fd	fd	fd	fd	
<i>Hapalemur griseus</i>	+	+	+	+		
<i>Lemur catta</i>						+
<i>Eulemur fulvus collaris</i>	+	+	+	+	+	
<i>Propithecus verreauxi verreauxi</i>	+					+
Total numbers of species	8	5	5	6	4	5

A plus sign (+) indicates that the given species was present; the abbreviation fd indicates that the presence of this species was determined by analyzing feeding damage to bamboo or wood.

* The presence of this species was determined only through the identification of its vocalizations.

cies in parcel 2 of the RNI d'Andohahela (Table 17-5). The body pelage was gray on the dorsum and whitish on the ventrum. A thin black dorsal stripe was often visible. The ears of *M. murinus* were large and prominent, in contrast to the smaller and more concealed ears of *M. rufus*.

Cheirogaleus major (Greater Dwarf Lemur)

Cheirogaleus major was observed from 440 to 1500 m by direct sightings during census walks in parcel 1 (Table 17-2) and was the most common primate species at these elevations. One in-

TABLE 17-3. Mean number of sightings per km transect and mean detection distances (m) (\pm standard deviation) of species (individuals) seen during nocturnal censuses in each elevational zone (parcel 1) in the RNI d'Andohahela.

Trail	Length of transects (m)	Number of censuses	Mean (\pm SD) detection distance (m)				Number of species
			<i>Microcebus rufus</i>	<i>Cheirogaleus major</i>	<i>Avahi laniger</i>	<i>Lepilemur mustelinus</i>	
440a	1200	4	1.3 (9.0 \pm 4.0)	2.9 (7.0 \pm 3.4)	—	—	2
440b	1150	4	1.7 (5.7 \pm 3.4)	2.8 (8.3 \pm 2.3)	0.4 (8.0)	0.9 (7.0 \pm 1.2)	4
810a	1750	4	0.9 (2.3 \pm 1.5)	0.7 (2.3 \pm 2.3)	—	—	2
810b	600	4	—	—	—	—	0
1200a	950	4	0.5 (3.5 \pm 0.7)	0.8 (5.0 \pm 1.0)	—	—	2
1200b	1000	4	—	1.5 (5.7 \pm 2.8)	—	—	1
1500a	1200	4	0.6 (1.0 \pm 0.0)	0.2 (10.0)	0.6 (1.0)	—	3
1500b	725	3	2.3 (1.2 \pm 2.1)	1.8 (6.3 \pm 1.3)	—	—	2
1500c	365	3	—	0.9 (1.0)	—	—	1
1875a	190	3	—	—	—	—	0
1875b	810	4	0.6 (2.3 \pm 1.1)	—	—	—	1
1875c	690	1	—	—	—	—	0
Overall mean detection distance (m)							
			4.0 \pm 3.7 n = 30	6.2 \pm 3.2 n = 40	3.8 \pm 3.8 n = 5	7.0 \pm 1.2 n = 2	

Detection distances are given perpendicular to the trail. n = number of individuals. A minus sign (—) indicates that the species was not detected.

TABLE 17-4. Mean number of sightings per km transect and mean detection distances (m) (\pm standard deviation) of species (individuals) seen during diurnal censuses in each elevational zone (parcel 1) in the RNI d'Andohahela.

Trail	Length of transects (m)	Number of censuses	Mean (\pm SD) detection distance (m)			Number of species
			<i>Propithecus verreauxi</i> (+ 'majori')	<i>Eulemur fulvus collaris</i>	<i>Hapalemur griseus</i>	
440a	1200	11	—	0.2 (8.0 \pm 1.0)	0.1 (15.0)	2
440b	1150	11	0.1 (10.0)	—	0.2 (6.2 \pm 5.0)	2
810a	1750	11	—	0.2 (5.0 \pm 6.2)	0.3 (2.8 \pm 3.2)	2
810b	600	10	—	—	0.2 (12.0)	1
1200a	950	13	—	0.7 (7.0 \pm 6.3)	0.1 (3.0)	2
1200b	1000	12	—	0.3 (9.3 \pm 7.4)	0.1 (3.0)	2
1500a	1200	13	—	—	0.2 (4.3 \pm 3.5)	1
1500b	725	12	—	—	0.1 (3.0)	1
1500c	365	11	—	—	0.2 (6.0)	1
1875a	190	9	—	—	—	0
1875b	810	10	—	0.1 (10.0)	—	1
1875c	690	5	—	—	—	0
Overall mean detection distance (m)						
			10.0 n = 1	7.3 \pm 5.6 n = 18	5.0 \pm 4.3 n = 18	

Detection distances are given perpendicular to the trail. n = number of individuals. A minus sign (—) indicates that the species was not detected.

dividual was also seen in the 1875 m zone outside survey walks (F. Hawkins, pers. comm.). The dorsal pelage of *C. major* was gray-brown with reddish tinges, and its underparts were paler, almost white. The head was gray-brown, and a small patch of white fur was located between the eyes, which were surrounded by marked dark rings. Most of the *C. major* observed had very fat tails.

Cheirogaleus major was generally observed alone. However, in five (15%) of 40 sightings two individuals were seen less than 3 m from each other in the same tree. We never saw more than two individuals in close proximity.

Avahi laniger (Eastern Woolly Lemur)

Avahi laniger was only sighted twice in parcel 1: once at 440 m and once at 1500 m (Table 17-3). It was never heard calling. Dorsal pelage was gray and the ventral parts were paler gray. The tail was gray-brown and darkened toward the tip. The face was brownish with a whitish band and distinct white patches above the eyes. The fur on the cheeks and throat was lighter colored. Two adults were seen in the same tree at 440 m. Two adults with a single offspring were observed at 1500 m. The group huddled together in the characteristic vertical resting posture in the fork of a

tree, and the infant was carried on the back of one adult.

Lepilemur mustelinus (Weasel Sportive Lemur)

Lepilemur mustelinus was also detected only twice, with each sighting at 440 m (Table 17-3). This species and *Avahi laniger* were the rarest species in parcel 1 of the RNI d'Andohahela. On each occasion an adult *L. mustelinus* with a single offspring on its back was seen. The dorsal and ventral fur of the two adult individuals was brown, and the tail color darkened distally.

Lepilemur leucopus (White-footed Sportive Lemur)

Lepilemur leucopus was very abundant in the spiny forest of parcel 2. The dorsal fur of *L. leucopus* was gray, with the underparts paler and sometimes tipped with brown. The arms and the tail were both reddish brown, whereas the thighs often showed gray tops. No infants were seen.

TABLE 17-5. Mean number of sightings, per kilometer transect, of diurnal (groups) and nocturnal (individuals) lemurs and mean detection distances (\pm standard deviation) of species seen in censuses in the spiny forest (parcel 2) of the RNI d'Andohahela.

Trail	Length of transects (m)	No. of censuses	Nocturnal censusus			Diurnal censuses			
			Mean (\pm SD) detection distance (m)		No. of species	No. of censuses	Mean (\pm SD) detection distance (m)	No. of species	
			<i>Lepilemur leucopus</i>	<i>Microcebus murinus</i>			<i>Propithecus v. verreauxi</i>		
120a	3500	3	1.1 (4.9 \pm 2.0)	0.6 (2.2 \pm 2.1)	2	9	1.3 (12.2 \pm 5.6)	1	
120b	3000	2	0.1 (2)	0.7 (4.2 \pm 1.5)	2	9	0.03 (13.5 \pm 9.2)	1	
120c	900	1	—	2.2 (4.0 \pm 5.7)	1	3	—	0	
			Total detection distance (m)					Total detection distance (m)	
			4.7 \pm 2.1 n = 13	3.2 \pm 2.5 n = 12				12.6 \pm 5.9 n = 7	

Detection distances (m) are given perpendicular to the trail. n = number of individuals. A minus sign (—) indicates that the species was not detected.

Daubentonia madagascariensis (Aye-aye)

Although we did not observe *Daubentonia madagascariensis* directly, their presence was evident in parcel 1 of the RNI d'Andohahela. Two types of damage attributable to this species were recorded between 440 and 1875 m. First, holes with notches around them that resembled incisor gnaw-marks were found in living and dead tree trunks in all elevational zones. Similar holes were also found in rotten pieces of wood on the ground. Second, we also found holes in bamboo stems wherever this plant was abundant. The bamboo internodes had been punctured and ripped back, producing a hole 1–2 cm long \times 0.5 cm wide that exposed the cavity within (as illustrated in Duckworth, 1993). Tooth-marks were present at the top of the rip. Occasionally the ripped-back slivers of bamboo were still attached to the holes. They were often moist and fresh, indicating that the holes had been gnawed recently. Most of the bamboo stems had several traces of excavation that were found at heights of 1–5 m.

At 810 m we found seeds of *Canarium madagascariense* (Burseraceae), a known food item for *Daubentonia madagascariensis* (Iwano & Iwakawa, 1988; Sterling et al., 1994; Goodman & Sterling, 1996), and checked them for feeding traces. All 37 seeds found and collected had been opened by rodents, and none exhibited traces characteristic of *Daubentonia*.

Hapalemur griseus (Bamboo Lemur)

Hapalemur griseus was found between 440 and 1500 m along the eastern slope of the Andohahela

Massif (Table 17-4). Its dorsal fur was dark gray, slightly tipped with olive-brown. The ventral fur was more brownish in color, and the crown was brownish red. These pelage characteristics did not correspond completely with those of typical *H. g. griseus* (Tattersall, 1982; Mittermeier et al., 1994). The individuals seen in the humid forest of RNI d'Andohahela were considerably larger than typical *H. g. griseus* and somewhat darker in pelage.

Hapalemur griseus was very cryptic. Often only two or three individuals were seen, but vocalizations indicated the presence of other group members. Group sizes ranged from one to six individuals, corresponding to previous reports with regard to this species (Petter et al., 1977; Tattersall, 1982; Pollock, 1986). Adults, subadults, and juveniles of less than 1 year (about 50% of adult body size) were seen. On one occasion an adult female was observed carrying a small brown-colored infant (head + body ca. 13–15 cm) on her back. *Hapalemur griseus* were observed feeding on bamboo. Their vocalizations were heard throughout the day, with a peak before dawn and in the early morning.

Lemur catta (Ring-tailed Lemur)

Lemur catta was heard but not seen during census walks in parcel 2 of the reserve. A group of *L. catta* was encountered, however, outside of the survey walks. The group consisted of six to eight individuals, with multiple adult males and only one clearly identified female. One well-grown in-

fant was seen riding on the female's back. One of the males had a damaged/infected left eye. The dorsal fur of *L. catta* was gray, as were the limbs and haunches. The face was white, with a black nose and dark triangular patches around the eyes. The tail showed the typical alternating black and white bands. Some members of the group were foraging on the ground, whereas the others stayed in the trees. Reaction to our presence varied from alarm calling to immediate flight.

Eulemur fulvus collaris (Collared Brown Lemur)

Eulemur fulvus collaris was found at altitudes of 440, 810, 1200, and 1875 m in parcel 1 of the RNI d'Andohahela. Surprisingly, we did not find them in the 1500 m zone. These lemurs showed a distinct sexual dimorphism in pelage coloration. Males had a brownish gray coat with a lighter colored ventrum, and a dark stripe down the back was often visible. The head, muzzle, and forehead were black. Males possessed a thick and dense beard that was orange to rufous in color and sometimes very bright. The dorsal fur color of female *E. f. collaris* was more rufous to brown, and the face was gray compared to that of the males, which was black. The beard of females was also reddish but shorter and less dense than that of males. Both sexes had completely dark tails. The four individuals seen at 1875 m had distinctly thicker pelage and a woollier appearance than those seen at the lower elevations. The single male we spotted in this zone also had a very bright orange beard and cheeks.

The small numbers observed and the few repeated sightings of *Eulemur f. collaris* within each transect zone made it impossible to determine the actual number of groups, and we are unable to give precise details on group size. When all records of this species are summarized, however, group size ranged from three to seven adults, with multiple males and females. Adults were seen carrying single offspring in virtually every group. Infants were always carried by adult females, with the single exception of an infant seen riding on the back of a male. No twins were observed.

This lemur was recorded only during diurnal censuses, but other observations during this survey showed the species to be active at night. *Eulemur fulvus collaris* should thus be considered cathemeral, pending further investigation.

Propithecus verreauxi verreauxi (Verreaux's Sifaka)

Propithecus verreauxi verreauxi, generally considered to be a species of only dry forest (Tattersall, 1982; Harcourt & Thornback, 1990), was seen in the humid forest at parcel 1 as well as in the spiny forest of parcel 2. The pelage coloration of the *P. v. verreauxi* found in the humid forest did not differ from that of those seen in the spiny forest. On the dorsum, outer thighs, and forelimbs the body fur was white. The inner and ventral parts were darker and somewhat grayish, and the lemurs had a brownish cap and a black face. In the 440 m zone of parcel 1, however, we recorded one group of six individual *Propithecus* that consisted of three typical white *P. v. verreauxi* forms and three "dark," or melanistic forms, previously called '*P. v. majori*' (Mittermeier et al., 1994). The three 'dark' individuals were also predominantly white, but they had dark brown fur on the back (dorsum) and on the inside of the extremities. Their ventral fur was brownish, compared to the grayish colored ventrum of the "white" animals. The face was black and the head cap was reddish brown to brown. All individuals were adult-sized, and one individual of the *P. v. verreauxi* "white form" carried a single infant on its back. Some members of the group started producing the "sifaka" vocalization when one observer approached. In general, however, the group remained relatively calm, and no flight reaction occurred during the 10 min of observation.

Opened Bamboo Segments

The majority of the 333 bamboo segments examined were empty. Eighteen (5.4%) segments, however, contained some form of animal life: white caterpillars (2–3 cm; $n = 7$), green caterpillars ($n = 4$), flatworms ($n = 1$), spiders ($n = 2$), and a frog ($n = 1$). In three sections (0.9%) we found large (3–5 cm) insect larvae, which are a preferred food item of *Daubentonia* (Sterling et al., 1994; Erickson, 1995). Water was found inside 33 (9.9%) of the 333 bamboo segments.

Discussion

During the surveys in the humid forest (parcel 1) of RNI d'Andohahela eight lemur species were

recorded: *Microcebus rufus*, *Cheirogaleus major*, *Avahi laniger*, *Lepilemur mustelinus*, *Daubentonina madagascariensis*, *Hapalemur griseus*, *Eulemur fulvus collaris*, and *Propithecus verreauxi verreauxi* (both white and melanistic). Previous workers have listed a variety of species present in the reserve (O'Connor et al., 1987; Nicoll & Langrand, 1989; Mittermeier et al., 1992, 1994). In addition to the species reported here, Mittermeier et al. (1992, p. 11; 1994, p. 280) listed *Propithecus diadema edwardsi*, *Propithecus diadema diadema*, *Lemur catta*, *Eulemur rubriventer*, *Varecia variegata variegata*, and *Indri indri* as occurring in this parcel. Their lists are clearly inaccurate. The geographical limit of *P. d. edwardsi*, *E. rubriventer*, and *Varecia* is north of the Mananara River near Farafangana, and the southern limit of *Indri* and *P. d. diadema* distribution is the Mangoro River, some 5° degrees latitude and 600 km north of the RNI d'Andohahela. *Lemur catta* generally occurs in the dry and spiny forests at relatively low altitudes (Tattersall, 1982; Harcourt & Thornback, 1990), but it was recently recorded by Goodman and Langrand (1996) above the forest line in the open summit zone (2520 m) of the RNI d'Andringitra. During the 48 days we spent surveying in the humid forest of the RNI d'Andohahela, however, we neither saw nor heard *L. catta*.

Of particular note was the observation of the generally strict dry forest lemur *Propithecus verreauxi verreauxi* during a diurnal transect in the 440 m zone of parcel 1. So far, the southeastern limit of the range of this *Propithecus* subspecies is the spiny forest of parcel 2 of the RNI d'Andohahela. Thus it is likely that some individuals from the western portion of the reserve occur in both forest types; whether their movements are seasonal is unknown. Additionally noteworthy was the fact that the sole group of *Propithecus* observed in parcel 1 contained three of the characteristic white forms and three melanistic forms (Tattersall, 1982, 1986). The melanistic form, previously regarded as subspecies '*majori*' of *P. verreauxi* (Elliot, 1907, 1913 in Tattersall, 1986), sometimes occurs within groups containing typical *P. v. verreauxi* (Petter et al., 1977; Tattersall, 1986), but its taxonomic status is poorly known. It seems clear that '*majori*' represents a polymorphic melanistic form of *P. v. verreauxi*. More work will define precisely the ecological requirements and needs of *P. v. verreauxi* in the humid forest.

Avahi laniger is found in numerous protected

areas (Mittermeier et al., 1994), providing a good picture of its latitudinal distribution. On the eastern slopes of the RNI d'Andringitra it was recorded up to 1625 m (Sterling & Ramaroson, 1996), on the RS d'Anjanaharibe-Sud up to 1260 m (Schmid & Smolker, 1998), and in parcel 1 of the RNI d'Andohahela up to 1500 m. The results from these studies indicate that *A. laniger* occupies a considerable elevational range.

The *Hapalemur griseus* individuals seen at the lower altitudes in parcel 1 of the RNI d'Andohahela were considerably larger than typical *H. g. griseus* and somewhat darker in pelage. One possibility is that they represent individuals of a putative southern form, *H. g. meridionalis* (Warter et al., 1987). The six animals upon which the description is based were captured 'about 10 km north of Fort Dauphin' (Warter et al., 1987, p. 51). *H. g. meridionalis* was described as having standard external features of *H. g. griseus*, with the exception of a darker coat. Head and body measurements were 30 and 32 cm; tail measurements were 36 and 31 cm. The karyotype of *H. g. meridionalis* was $2n = 56$, in comparison to $2n = 54$ of *H. g. griseus* (Warter et al., 1987). Confirmation of the taxonomic status of the lemurs we observed in parcel 1 was not possible, however, and will require additional morphometric and genetic data. Thus we refer to the observed bamboo lemurs simply as *Hapalemur griseus*.

The encounter rate of *Lepilemur mustelinus* was extremely low, with only two sightings in the lowest transect zone. The people living in the vicinity of the reserve never mentioned hunting *Lepilemur*, and it therefore seems unlikely that this is the cause of their rarity. *Lepilemur* are folivorous lemurs with very specialized microhabitats (Ganzhorn, 1989).

The average number of *Eulemur fulvus collaris* sightings increased with elevation (except at 1500 m). We received reports that several hundred of these lemurs are hunted in the lower portions of the reserve each year (B. Randriamampionina, pers. comm.). The 440 m zone was within a 3 hr walk of the nearest village, a fact that might explain the low encounter rate and the flight reaction of this species. Hunting pressure on brown lemurs is widespread, and it is known to affect group size and behavior (Duckworth et al., 1995; Schmid & Smolker, 1998). It is difficult to explain the absence of *E. f. collaris* in the 1500 m zone because they were seen within all of the lower zones as well as at 1875 m. We suspect that they would have been detected with a more intensive sam-

pling effort. The thick pelage of the *Eulemur* observed at the summit camp suggests adaptation to the high mountain and meteorologically more extreme zone of the massif.

Signs of *Daubentonia* were recorded at every site censused, from 390 m to 1920 m. This last elevation may represent the highest altitude at which this species has ever been recorded. Just below the summit of Pic Trafonaomby there was a large amount of bamboo, and there were numerous signs of *Daubentonia* feeding on prey cached in the stems of this plant. Identical traces were found in bamboo at the RNI de Marojejy (Duckworth et al., 1995). Whenever bamboo was abundant we found numerous bamboo stems that had been damaged by aye-ayes, presumably preying on insect larvae. It was not surprising that we found few insect larvae in the bamboo segments we opened, because these segments may well have been investigated by aye-ayes just prior to our arrival and were left intact because they were empty. Pollock et al. (1985) reported *Daubentonia* feeding on shoots of bamboo.

It has been suggested that the distribution of *Daubentonia* is closely tied to that of *Canarium* (Iwano et al., 1991; Sterling & Ramaroson, 1996), and that the seeds are, at least during the hot dry season, one of this species's most commonly eaten foods (Sterling et al., 1994). In the humid forest of the RNI d'Andohahela, however, *Canarium* was exceptionally rare. Only two *Canarium* trees were found in 5 ha of plots censused across the elevational gradient, one at 810 m and one at 1200 m. None of the 37 seeds examined bore traces of *Daubentonia*. *Daubentonia* density may thus be low in parcel 1 due to an important food source being locally rare, or *Canarium* may not be as critical to *Daubentonia* in Andohahela as studies from Nosy Mangabe suggest.

For the spiny forest of parcel 2 of the RNI d'Andohahela, Mittermeier et al. (1994) listed six lemur species. From this list we recorded five species: *Microcebus murinus*, *Lepilemur leucopus*, *Lemur catta*, and *Propithecus verreauxi verreauxi* by direct observations and *Phaner* by vocalizations. We did not locate the sixth species, *Cheirogaleus medius*. The apparent absence of this last species is surprising because it has been recorded previously in Andohahela (O'Connor et al., 1987; Nicoll & Langrand, 1989), although it is reported to be rare in both Berenty and Beza Mahafaly (Sussman & Richard, 1986; Mittermeier et al., 1994). It seems unlikely that the absence of *C. medius* is due to sampling error. During the sur-

vey all nocturnal species present were generally recorded within 3 hr of censusing. Thus, the 18 hours of nocturnal census work at parcel 2 should have been sufficient to record *Cheirogaleus*, had it been there in any reasonable numbers. It may be difficult, however, to obtain a complete species list for a region within a short time span if lemur activity is strongly affected by seasonal variation. This is particularly so for *C. medius*, which undergoes a period of prolonged torpor from April or May until mid-September (Martin, 1972; Petter-Rousseaux, 1980). The survey in parcel 2 was undertaken between 8 and 13 December, however, so hibernation cannot account for this species' absence. The ambient and physiological conditions determining the end of hibernation are still unclear, but rainfall seems to have a strong influence on emergence date (J. Fietz, pers. comm.). At the beginning of the 6 days that we spent in the spiny forest, we had exceptionally heavy rain, so *C. medius* could be expected to have emerged and to have been recorded during our surveys.

Phaner furcifer was heard on two separate occasions; four different individuals could be localized on one of these occasions. Vocalizations are an important part of social communication in this species, and individuals are generally in constant vocal contact (Charles-Dominique & Petter, 1980). We never observed *Phaner* directly, perhaps because they occur at heights of 12–15 m, where they are difficult to detect (Petter et al., 1971). In fact, there are few records of *Phaner* being sighted in parcel 2, and records of its occurrence have largely relied upon the identification of its vocalizations (Russell & McGeorge, 1977; O'Connor et al., 1987). *Phaner furcifer* can frequently be heard calling near the village of Hazofotsy (Feistner, unpubl. data; M. Pidgeon & S. Goodman, pers. comm.). It is not known which subspecies occurs in this region.

Rapid biodiversity assessment techniques to decipher the patterns of species distribution and population abundance are problematic for several reasons. First, sampling times often differ from site to site, as do climatic conditions. For instance, during our survey work in the 810 m zone of parcel 1, heavy rain and fog interfered with sampling on half of the census nights, and few lemur sightings were made. Second, in upland areas the trails often cross bare, rocky terrain that is unlikely to support lemurs. At some sites in this survey, the steep relief meant that transect lengths were short to keep within the elevational limits. In lieu of repeating short transects several times, fewer rep-

etitions of much longer transects would have been preferable. In the 1200 m zone the same groups of *Eulemur f. collaris* were encountered repeatedly on one of the transects, violating the assumption of independent sampling necessary for calculation of density (Brockelman & Ali, 1987; Whitesides et al., 1988). Overall, small sample sizes mean that it is difficult to accurately determine group size and composition for diurnal lemur species. In addition, rare species may not be detected at all within the available sampling time. These factors need to be considered when analyzing and interpreting rapid census data.

The lemur diversity of only eight species along the eastern slope of Andohahela is low in comparison to other humid forest sites at lower latitudes, where reliable data are available. For example, 13 species have been recorded in the RNI d'Andringitra (Sterling & Ramarason, 1996), 12 in the Parc National de Ranomafana (Mittermeier et al., 1994), 13 in the RNI de Zahamena (Mittermeier et al., 1992), 10 on the Masoala Peninsula (Sterling & Rakotoarison, 1998), and 11 in the RS d'Anjanaharibe-Sud (Schmid & Smolker, 1998). Only one species of *Hapalemur* is listed for parcel 1 of the RNI d'Andohahela, compared to the eastern slope of the RNI d'Andringitra, which supports three *Hapalemur* species. When the species observed in the western spiny forest of parcel 2 are added, the RNI d'Andohahela has a total of 13 lemur taxa.

Apart from the relatively low diversity of lemurs, the abundance of several species was strikingly low. Although we did not calculate actual lemur densities, the encounter rate for both diurnal and nocturnal humid forest species was exceptionally low. For example, in the 1875 m zone there was on average one nocturnal lemur sighting per 2.3 km of transect. The lowest encounter rate for diurnal lemurs was in parcel 1 at 1500 m, where there was an average of one sighting per 5.5 km walked.

Despite the comparatively low diversity and density of lemur species, it is clear that Andohahela is important for the conservation of both wet and dry forest primates. The eastern humid forest of the RNI d'Andohahela (parcel 1) is the only protected area in Madagascar where *Eulemur fulvus collaris* occurs naturally. Despite this it was reported to us that large numbers of this taxon are hunted every year. In the spiny forest, the environment was being degraded by people and their livestock. We often encountered people, goats, zebu, dogs, and even cats in the reserve. Grazing

and browsing by the ungulates prevents plant regeneration and growth, and trampling crushes and degrades the flora and soils. Domestic carnivores and feral rats can have a significant impact on bird and reptile faunas (Iverson, 1978; Case et al., 1992). The ongoing deforestation of Andohahela's western spiny forest also threatens the eastern humid forest slopes of the massif. In the 1875 m zone, the sclerophyllous forest below Pic Trafonaomby (1956 m) had been burned just a few days before our arrival. Blackened bamboo stems and tree trunks were left, still smoking from the fire. Below the summit zone was a plateau system that had clearly been modified by burning and cattle grazing for some considerable time. Human disturbance had thus already advanced up the western slope of the Andohahela Massif, where most of the forest was gone already.

In order to draw up conservation management plans for Madagascar's unique flora and fauna, it is important to investigate the diversity and distribution of endemic plants and animals. Even with such apparently well-studied animals as lemurs, distributional and elevational limits are poorly known for many taxa. Biological inventories are important in providing this information. Indeed such work has already resulted in the resurrection of synonymized species and the description of new lemur taxa (Schmid & Kappeler, 1994; Zimmerman et al., 1998). Given the speed with which habitats are being degraded, conservation decisions may need to be made rapidly. Devising efficient methods of undertaking biological inventories, including rapid assessments of primate distribution, population dynamics, and conservation status, is especially important when time is short, resources are limited, and the need for remedial conservation action is acute.

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Gazetteer of Localities Mentioned in the Text*

Locality	Longitude E		Latitude S		Elevation (m)
	°	'	°	'	
Alaotra, Lac	48	30	17	30	
Ambatomaniha, Col d'	46	45	24	46	~1000
Ambatovaky, RS	~49	15	~16	42	
Amboanemba	46	28	24	41	225
Amboasary-Sud	46	24	25	03	
Ambohimitambo	see Ambohimitombo				
Ambohimitombo	47	23	20	43	
Ambohitantely, RS	~47	16	~18	09	1450–1660
Ambositra	47	15	20	30	
Ambatorongorongo	46	47	25	04	
Ambovombe	46	05	25	11	
Ampamakiesiny, Col d'	46	50	24	31	1375
Ampanihy	44	45	24	42	
Ampitambe†	47	46	20	22	
Anadabolava	46	19	24	13	200
Analalava Forest	47	19	24	13	20–50
Analamazaotra, RS	48	28	18	28	930–1040
Analavelona	44	12	22	41	
Anandrano	46	59	24	57	10
Anatranatra	46	39	24	18	325
Andaza	46	34	24	03	315
Andohahela, Pic	46	42	24	38	1935
Andrahomana Cave (Grotte)	46	40	25	50	
Andrandrivola Forest	49	36	15	46	450–625
Andranohela River	~46	47	~24	38	
Andranomay Forest	47	57	18	29	1300
Andranomintina	50	19	15	44	
Andranondambo	46	35	24	25	
Andringitra, RNI	46	54	22	14	
Anjanaharibe-Sud, RS	~49	26	~14	42	500–2064
Anjozorobe	47	52	18	24	
Ankafana	see Ankafina				
Ankafina	47	12	21	12	
Ankapoky Forest	46	31	24	59	
Ankarafantsika, RNI	~46	57	~16	09	80–330
Ankaratra	47	12	19	25	
Ankazomanga	46	37	24	03	430
Ankazondrano	see Trafonaomby				
Ankepotsy	46	43	24	33	1550
Anony, Lac	46	31	25	08	0–10
Anosibé An'ala	48	03	18	55	
Anosy River	not located				
Antalaha	50	16	14	53	
Antanifotsy	46	58	24	59	
Antsirana	see Antsiranana				
Antsiranana	49	17	12	16	
Antsovela	46	28	25	05	20
Bakika	see Ebakika				
Baly	45	17	16	05	
Beampingaratra	46	51	24	28	
Beampingaratra Mountains	see Anosyenne Mountains				
Belavenoka	47	05	24	50	20
Bemangidy	47	14	24	34	~100
Bemangily	see Bemangidy				
Beraketa	45	42	24	11	
Berenty, RP	46	17	24	59	
Berohanga	46	36	24	39	550
Besomosoy	46	28	24	06	275

Gazetteer

Locality	Longitude E		Latitude S		Elevation (m)
	°	'	°	'	
Betanimena	46	39	24	48	120
Betenina	46	25	24	25	325
Betroka	46	06	23	16	
Bevilany	46	36	25	01	~100
Bevoay	46	49	24	40	100
Bezavona	46	58	25	01	
Camp 1 (1995)	46	45.9	24	37.6	440
Camp 2 (1995)	46	44.3	24	35.6	810
Camp 3 (1995)	46	44.1	24	35.0	1200
Camp 4 (1995)	46	43.9	24	34.2	1500
Camp 5 (1995)	46	43.3	24	33.7	1875
Camp 6 (1995)	46	36.6	24	49.0	120
Didy	48	32	18	07	
Diégo-Suarez		See Antsiranana			
Ebakika River	47	10	24	43	
Efaho River	46	52	25	48	
Ejeda	44	31	24	20	
Elakelaka		not located			
Eminiminy	46	49	24	41	~100
Enakara	46	54	24	37	
Enosiary	46	49	24	40	
Erombo, Lac	46	37	25	09	0-15
Esira	46	43	24	20	400
Esomony	46	38	24	30	530
Etsilitsily	46	46	24	50	
Ezoambo	46	52	24	49	25
Fanjahira	46	54	24	55	
Fanovana	48	34	18	55	
Farafangana	47	50	22	49	
Fenoervo	46	53	24	42	75
Fort-Dauphin		See Tolagnaro			
Grand Lavasoa	46	45	25	06	823
Hazofotsy	46	33	24	49	~100
Ifarantsa	46	52	24	56	20
Ifotaka	46	08	24	48	60
Ihazofotsy		see Hazofotsy			
Ikongo Forest	43	33	21	47	
Iloty	46	37	24	38	525
Imanombo	45	46	24	28	215
Imonty	46	41	24	49	175
Isaka-Ivondro	46	52	24	48	50
Isedro, Col de		see Ambatamaniha, Col d'			
Isedro Trail	46	46	24	46	
Itapera	47	07	24	53	0-20
Itaranta River	46	29	25	01	
Itrafanaomby		see Trafonaomby			
Ivohimanitra	47	25	20	42	
Kalambatritra, RS	46	29	23	28	1300-1500
Kirindy Forest	44	43	20	03	
Lakato	48	22	19	03	1050
Mahajanga	46	19	15	43	
Mahamavo	46	43	24	46	370
Mahamavo, Col de	46	42	24	38	
Majunga		see Mahajanga			
Malahelo Forest	46	47	25	05	
Manafiafy	47	11	24	45	0-20
Manajary	48	20	21	13	
Manakara	48	01	22	08	
Manambaro	46	49	25	02	

Gazetteer

Locality	Longitude E		Latitude S		Elevation (m)
	°	'	°	'	
Manampanihy River	~46	58	~27	35	
Mananara, RB	49	44	16	23	
Mananara River	46	33	24	50	
Manangotry, Col de	46	52	24	45	~830
Manantantely Forest	46	55	24	59	50-600
Manantenina	47	19	24	17	30
Mandena	47	00	24	58	0-20
Mandrare River	46	24	25	03	
Mandromodromotra River	47	02	24	55	
Mangoro River	48	45	20	00	
Manjakatombo	47	26	19	20	
Manombo, RS	47	44	23	02	0-137
Mantadia		see Mantady			
Mantady, PN	48	27	18	51	
Maroantsetra	49	44	15	26	
Marojejy, RNI	~49	15	~14	26	75-2133
Maromby	46	35	24	24	345
Marotoko River	46	39	24	44	275
Marosohy Forest	46	49	24	34	350-1300
Marosohy, Col de	46	48	24	32	~1300
Marovoay	46	39	16	06	
Marovony Forest	47	20	24	05	50-100
Masoala Peninsula	~50	10	~15	38	
Montagne d'Ambre	~49	10	~12	37	
Montagne d'Ambre, PN	~49	10	~12	37	
Moramanga	48	12	18	56	
Morondava	44	17	20	17	
Nahampoana	46	58	24	58	75-300
Nandihizana	~47	10	~20	50	
Nosiarivo Forest	47	18	19	21	
Nossi-Bé		see Nosy Be			
Nosy Be	48	15	13	20	
Périnet	48	25	18	56	
Petriky	46	53	25	04	0-40
Pic Boby	46	53	22	11	2658
Pic d'Ivohibe (Ivohibe)	46	57	22	31	
Pic d'Ivohibe (Bemangidy)	47	12	24	33	
Pic d'Ivohibe, RS	~46	59	~22	32	
Pic Maromokotro	48	58	14	01	2876
Pic St. Louis	46	58	25	01	530
Ranoholo River		see Andranohela River			
Ranomafana, PN	47	28	21	16	
Ranomafana Atsimo		see Ranomafana de Sud			
Ranomafana du Sud	46	57	24	34	
Ranomafana-Sud		see Ranomafana du Sud			
Ranomafana-Tanosy		see Ranomafana du Sud			
Ranopiso	46	42	25	04	
Ranopiso, Col de	46	39	25	02	~300
Sakamalio	46	41	24	32	750
Sakatay		see Hazofotsy			
Sedro		see Isedro			
Soanierana	46	52	24	48	20
Ste. Luce		see Manafiafy			
Talakifeno	46	41	24	50	145
Tanandava	47	03	24	24	
Tanatana, Col de	46	51	24	44	~750
Tapera		see Itapera			
Tarantsy River	46	34	25	00	~70
Tolagnaro	46	59	25	01	0-40

Gazetteer

Locality	Longitude E		Latitude S		Elevation (m)
	°	'	°	'	
Trafonaomby, Pic	46	44	24	33	1956
Tranomaro	46	29	24	36	
Tsaratanana, RNI	~48	51	~13	59	227–2876
Tsilotsilo, Col de		see Etsilitsily			
Tsivory	46	05	24	04	
Varavara, Pic	46	43	24	30	
Vinanitelo	47	16	21	43	
Vohibaka	46	46	24	32	
Vohimena Mountains	~47	00	~24	50	
Vohisandria	46	39	25	10	
Vondrozo	47	20	22	49	
Zahamena, RNI	~48	50	~17	40	750–1512
Zombitse, PN	~44	40	~22	47	485–825

* For geographical localities such as rivers, large reserves, and mountain ranges an intersection of coordinates is given that allows for easy location on maps. The information in the body of the gazetteer is based partially on data from U.S. Board on Geographic Names (1955) and Viette (1991). Abbreviations for protected area designations: PN = Parc National, RB = Réserve de Biosphère, RNI = Réserve Naturelle Intégrale, RP = Réserve Privée, and RS = Réserve Spéciale.

† Based on Carleton and Schmidt (1990).

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Field Museum of Natural History
Roosevelt Road at Lake Shore Drive
Chicago, Illinois 60605-2496
Telephone: (312) 922-9410

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